CYTOGENETICS
AND
PLANT BREEDING

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By

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FOREWORD

Until very recently plant breeding was considered more an art than a science. This has however changed and it is now recognised that a successful plant breeder must have a sound knowledge of the principles in such allied sciences like genetics, cytology, taxonomy, statistics, etc. Except probably in U.S.S.R. the chromosome basis of heredity is now universally accepted, and a knowledge of this basis is considered essential to the plant breeder. The value of plant breeding is assuming an ever increasing importance in the improvement of agriculture of every country, and its importance to India whose main industry is agriculture need not be emphasised. The importance of the application of genetic principles to methods of plant breeding is now well understood. Several of the universities in India have a good school of cytology in their botany departments but it is the teaching of genetics and the cytogenetic principles that are of great importance to plant breeding that has been practically neglected. It is no exaggeration to say that until very recently a student can take Honours degree in Botany in some of the universities without any knowledge of the important agricultural crops of the country and how they grow. While taxonomy is very well taught in most universities its integration to the study of the wild and cultivated species of agricultural crops is never attempted. The study of important crops is however now included under economic botany in the curriculum of studies for a degree in botany in every university. But so far as genetics is concerned the students get nothing beyond a few lectures on mendelism and that too with the classical examples of peas, maize and *Drosophila* mentioned in the standard text books published abroad. It can, however, be said that the teaching of genetics and plant breeding is done somewhat better in the several agricultural colleges of the country which are all affiliated institutions to the universities in their respective provinces. Genetics of crop plants forms part of the curriculum of studies under agricultural botany in these institutions. The advantages the agricultural colleges have over the universities is that there are crop specialists dealing with genetical and plant breeding problems of crops and there is always plenty of live segregating material growing in the fields which the students can observe for themselves. In some of these agricultural institutions either the whole teaching of genetics is entrusted to a crop specialist or the several crop specialists dealing with rice sugar-cane, cotton, millets and pulses deliver a few special lectures to the students on the genetics of their particular crops. I am specially referring to the position in the agricultural college at Coimbatore.

Even in the agricultural colleges, unless the teacher takes special pains to gather examples from the published papers dealing with local crops, the teaching cannot be considered any better than in the universities. Although there are good text books on genetics and plant breeding, particularly those published in U.S.A. it can be said that there exist no suitable text book on many of the agricultural sciences specially adapted to tropical and sub-tropical

plants and to tropical conditions which makes the teaching of this particular science to students a difficult undertaking. It must, however be admitted that the preparation of text books and teaching of any science should follow a period of extensive and intensive investigations at several experimental stations and special laboratories so that the results could be compiled and taught to the students. So far as genetics and plant breeding are concerned the work done in India during the last thirty years can compare very favourably with similar work done in any of the more advanced countries of the west. But the results have remained scattered and buried in several departmental reports and scientific reports of experimental stations. Even the information published in the scientific journals is piece-meal and incomplete with the result that it has not attracted the attention it probably deserves. The absence of a comprehensive and critical account of the available results dealing with genetics and plant breeding problems of the tropical crop plants, makes the work of the teacher who has to teach these subjects to the students extremely difficult.

The senior author of the book has been connected with teaching botany at the agricultural college, Coimbatore, during the last twenty-five years, and the junior author for over four years after some years experience in plant breeding research in rice and cotton. The authors have, in the preparation of this text utilised not only the data published in the Indian journals, but also some of the unpublished data available with the crop specialists at the Coimbatore research institute. The most important salient feature of the book is that most of the examples included to explain genetic segregation, special cytological phenomenon, breeding for disease resistance, conduct of yield trials, etc., are all from data relating to tropical crop plants collected in India itself. The book can therefore be said to meet a long felt need for a suitable text book on genetics and plant breeding for the students of the agricultural colleges. There is no doubt that the book will also prove suitable to students in the universities as a useful text book. The attempt of the authors in the preparation of this book is the first of its kind in the country and I am sure it would be welcomed by all interested in these sciences.

CUTTACK

K. RAMIAH

2nd December, 1947

PREFACE

The science of Cytogenetics is a modern triumph over Nature which has enabled Man to revolutionize crop production. The old time plant breeder achieved great results through patient observations of the workings of Nature. He had to stoop to Nature's commands to conquer her ; but his modern counterpart dictates what he wants and endeavours to mould the crop to suit the ideal he has in view. Man has learnt some of the inner secrets of Nature. He can now unerringly hope to combine the desired genes from different organisms ; he can effect chromosomal aberrations and evolve new types of plants and animals, some of great economic importance.

Cytogenetics has therefore a great part to play in shaping a new world of balanced abundance. Messrs. S. N. Chandrasekhara Ayyar and S. V. Parthasarathy, the authors of the book, deserve warm congratulations in presenting a scientific treatise like a romance that it is. The book has an added value to laymen, students and research workers in India, as it is a complete survey of the genetic work already done in respect of familiar plants in the country.

I trust the book will stimulate the minds of enthusiastic workers to make concerted efforts to improve the efficiency of Indian Agriculture through scientific crop breeding.

MADRAS
19—2—1948

M. S. SIVARAMAN
Director of Agriculture.

AUTHORS' PREFACE

Though genetics in its application to agriculture is less than five decades old yet it is the most potent science in the improvement of agriculture. This science is being intensely developed by the universities in the west by their work on animals and plants—such as *Drosophila* and *Datura*—which may not be directly of great economic importance. In this country the universities have not paid much attention to the development of this science. Ramiah (1941) in his Presidential address to the section of agriculture of the Indian Science Congress and again in the foreword to this book has emphasised the importance of teaching this Science in the universities in this country.

The research and teaching staffs of the department of agriculture, are generally different the one having little to do with the other. Therefore the researches in the various agricultural research institutes have always lain buried in the journals while the students in the colleges are taught examples from foreign texts. The authors therefore felt that there existed a great need for a text in which the up-to-date researches and advances made in this country could be presented in a form which would be useful. It is with this object that an attempt was made to bring up this book before the public. We are not unaware of the fact that there are more competent men than ourselves in the field to deal with such a problem. We cannot do better than to quote Huxley (1945) who in his preface to the book Evolution—the modern synthesis, states—" 'The writing of it has so much clarified my own thinking, and the discussion of the problem that arose with my colleagues has resulted in so many ideas and points of view which were novel both to them and to myself, that I am encouraged to believe it will be of general service'—and since others better equipped than I seem reluctant to attempt the task, I have tried my hand at it." Such competent men in this country are the plant breeders and crop botanists of the agricultural departments, but such men are always busy with other urgent problems. As professors of one of the premier agricultural colleges of this country we felt that we owed a duty to the students in providing a suitable text book to give them up-to-date knowledge of the science. The importance of the text books in colleges cannot be over emphasised. Burns (1943) stated " No science rises above the level of its text books or of its teachers in the more important universities."

If this text book contains anything useful to the student, the credit is to the host of research workers—present and past who struggled hard to develop this science in this country.

In the preparation of this book, we owe a great deal to Dr. N. Parthasarathy who evinced keen interest in this work and but for whose help, we could not have ventured in this direction. He read through the manuscripts and proofs and suggested many valuable points both in regard to presentation and subject matter. He has been delivering special lectures in cytology to the students

of the agricultural college at Coimbatore. For the chapters on cytology in this book, we have drawn liberally from his lectures, with his kind permission and consent. We feel that our gratefulness to him cannot be adequately expressed by words in these pages.

We are thankful to the Government of Madras and to the Director of Agriculture, Madras, for granting us the necessary permission for bringing out this publication. Our thanks are due to Sri R. Balasubramaniam and Sri S. M. Kalyanaraman for the help rendered in the preparation of the chapters on statistics. We are indebted to the various research officers and crop specialists at Coimbatore for helping us with photographs, charts, etc., which are reproduced in this book and duly acknowledged in the pages of the text. Their researches have always been inspiring to us and to the students of this college.

We are indebted to the Government of India, and to the Indian Council of Agricultural Research for permitting us to reproduce scientific data and photographs published in their scientific journals such as Agricultural Journal of India, Indian Journal of Agricultural Science, Agriculture and Livestock in India and Indian Farming. They were also very kind in lending to us some of the blocks available with them. We should in this connection mention the help rendered by Sri N. L. Dutt in enabling us to liberally illustrate our book with photographs on sugarcane.

We are indebted to the Editors of Current Science, Proceedings of the Indian Academy of Sciences, and the Indian Journal of Genetics and Plant Breeding who permitted us to reproduce photographs from these journals. They were also kind enough to lend us the blocks wherever possible. We are thankful to the Editor of the Journal of Genetics for the kind permission granted to us to reproduce illustrations from this journal.

Our thanks are due to the various authors from whose publications the tabular statements have been reproduced. We may however mention the names of a few authors from whose publications we have drawn liberally. Iyengar, R. L. N., for tables 23, 24, 25, 26, Kesava Iyengar, N. for tables 39, 44, 45, 46, 56, Dr. Pal, B. P. and his co-workers for tables 37, 40, 93, 101, 102 and 103, Ramanatha Iyer, V. and his co-workers for tables 21, 22, 32, 54, 82, 83 and 96, Dr. Ramanujam, S. for tables 35, 36, 38, 41, 42, 48, 49 and 62, Ramiah, K. and his co-workers for tables 6, 14, 27, 52, 61, 65, 66, 72, 81, 86 and 97, Rangaswamy Ayyangar, G. N. and his co-workers for tables 3, 15, 18, 34, 73, 74, 75 and 76. We have to mention here as a word of caution that the list of disease resistant varieties in table 100 which is reproduced after Mathusuthan Rao (1936) may not still be up-to-date in the field especially after nearly a decade of evolutionary struggle between the varieties and the pathogens.

We are indebted to Professor R. A. Fisher and Dr. F. Yates, also to Messrs. Oliver and Boyd Ltd., Edinborough for permission to reprint tables Nos. III, IV and V from their book Statistical Tables for Biological, Medical and Agricultural workers.

Appendix IV is compiled from the gene symbols published by Ramiah and Kadam (1943) on rice, Rangaswamy Iyengar *et al* (1942) on cholam, and Hutchinson and Silow (1939) on cotton.

In the compilation of Appendix V, various publications have been consulted. At the time when this went to press we came across the publication Chromosome Atlas of Cultivated Plants by Darlington and Janaki Ammal. As far as possible we checked up the numbers reported here. This appendix is intended to provide only a preliminary reference by the students and hence authorities for this have not been furnished.

Since this book is mostly intended for beginners and students of colleges we omitted direct references to literature in the body of the text. Therefore a list of publications which were useful to us directly or indirectly in the preparation of this text is provided as Appendix VII. Some omissions in the preparation of this appendix were kindly brought to our notice by Sri K. Ramiah and we have tried our best to rectify the same. It is hoped to make this more perfect in the next edition.

We are thankful to Sri K. Ramiah, Director, Central Rice Research Institute, Cuttack for kindly consenting to write the foreword for this text. We are also thankful to Sri M. S. Sivaraman, Director of Agriculture, Madras for writing up the preface.

We also acknowledge our thanks to Sri Daniel Sundararaj and Sri K. Meenakshisundaram and Sri S. R. Ganguly for help rendered in the preparation of the appendices and index.

Lastly we wish to thank the typist, the artist, the publishers and the press for their kind co-operation in the various stages of the preparation of this text. They have all struggled under war time conditions when there was dearth for men and material in the market but for which the quality of paper and print would have been more attractive.

To all our readers our request is that they adopt the attitude of the proverbial swan and take the useful part and reject the useless part in text. We assure them that with their co-operation we will endeavour our best to improve everything in the next edition.

COIMBATORE, S. N. CHANDRASEKHARAN

October, 1947 S. V. PARTHASARATHY

PUBLISHERS' NOTE

We are thankful to the Scientific and student world for the kind reception given to the first edition of this book. We are glad to bring out the second reprint edition with slight changes in chapter 12 and addition of chapter 26—Human Genetics. We trust we will be able to revise and enlarge the third edition.

PUBLISHERS.

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Chapter I

HISTORICAL RESUME

INTRODUCTION—PRE-MENDELIAN—MENDELIAN—RECENT ADVANCES

Introduction.—The rediscovery of Mendel's Laws in 1900 laid the foundation for the development of a new Biological Science, viz., *Genetics*. Like every other art and science which distinguishes the modern world from what it was in the dark ages, the recently developed new branch of science is enlarging our knowledge regarding the nature of life. When man gave up his nomadic life and settled down in a place, he began to improve the various forms of life to meet the demands of his food, clothing and other requirements. This art of breeding of plants and animals was therefore very ancient and was practised without the knowledge of principles underlying selection. All the cultivated plants and domestic animals of the present day are the products of such selection practised by our ancestors on wild life. Based on sheer experience they have achieved some success. From the Chinese records it is known that many varieties of rice were under cultivation in China, since 5,000 B.C. The excavations at Mohanja Daro showed that cotton was cultivated in India long prior to 5,000 B.C. The Egyptian mummies show that wheat was under cultivation there since a long time.

Man selected those plants that were useful to him in his multifarious requirements and rejected the rest. He paid more and more attention to those that were of importance to him. While man artificially maintained plants and animals of economic importance and also improved them by successively selecting the best, the uncared for wild life were also under selection by Nature. While man selected plants and animals for the characters which best suited his needs, irrespective of the value of the character to the organism, the survival of wild life depended on their adaptation to natural condition. *Thus, Natural selection and artificial selection by man were not in the same direction and hence it is that man has taken great care to preserve his own selections and guard them against the opposing forces of Nature.* It is as a result of such care and attention that very valuable cultivated plants have been evolved and these have come to differ in many respects from their wild ancestors. In many cases the wild types have become extinct. The vast survey of wild and cultivated plants made by Vavilov has disclosed some probabilities of the origin of cultivated plants.

In outlining the history of Genetics and Plant Breeding, the period may be divided into (1) Pre-Mendelian (2) Mendelian and (3) Recent advances.

2. **Pre-Mendelian.**—In this period may be included all the important discoveries prior to 1900.

Variation and Evolution of new species were first studied by Lamarck (1744-1829). From plant to plant and from species to species there are variations. Lamarck assumed that there are three main causes for variations to arise (*a*) through conscious effort (*b*) by changed environment (*c*) use and

disuse of various organs. Variations acquired in the life-time of the organism are transmitted to the progenies and thus in course of time new species arise. But Lamarckism was disproved by Weismann (1834–1914) and his conclusions are that the acquired characters are not inherited. His conclusion is of fundamental importance. The concept underlying this theory is that all organisms are made up of *somatoplasm* and *germplasm*. The former builds up the body and the latter is responsible for transmitting the characters to the progeny. Germplasm is immortal and continuously streams from generation to generation while somatoplasm serves as a temporary shelter for the former and by itself is incapable of transmitting the characters. He definitely proved that acquired characters are not inherited and recognised that nuclei of the gametes are the seats of heredity. *Thus in a plant some of the variations are hereditary and some are acquired.*

The most plausible explanation which caught the imagination of all biologists came from Charles Darwin. Darwin was a keen observer of Nature and he published the book " Origin of species " in 1859. The controversies raised over his conclusions were mainly based on speculations and not on careful experiments and data. They did not clearly understand how the characters were transmitted from parents to the progeny. Darwin himself put forward a fantastic *theory of pangenesis*. He assumed that the heredity bearing particles or *pangenes* collect together to form the germ cells. He believed in the inheritance of some acquired characters. According to him variation is a universal phenomenon occurring in nature. *In all organisms, over-production is observed and this leads to competition, struggle for existence and survival of the fittest through Natural selection.* The unfit are eliminated in the competition. The qualities which contributed to the success of the survivors in the competition are continued in the progenies.

Recent researches indicate that a modified form of Darwinism is the principle governing Evolution. This is sometimes referred to as *Neo-Darwinism.*

The *cell theory* (1838–39) of Schleiden and Schwann is an important pre-mendelian conception in biology. It is now more than a century since cell is recognised as the unit of structure and function. In 1665, Robert Hooke examined a thin slice of cork under his microscope. He described it as made up of " cell." The term cell is applied since then and it is a compartment filled with protoplasm. Robert Brown (1831) described nucleus and Hugo Von Mohl (1846) showed that cytoplasm is made up of living substance termed " protoplasm." Gruber (1883) by his work on *Stentor* showed that the nucleus is the most vital part of the protoplasm. It is the control centre for all activities of the cell. Between the first publication of Mendel's laws in 1866 and its rediscovery in 1900 many important discoveries were made. These were helpful not only in the application of Mendel's laws but also soon laid the foundation for cytogenetics. Hertwig (1875) and Strasburger described the male nucleus and traced its course in fertilisation. The constancy for chromosome number for any species and their multiplication by longitudinal splitting were explained by Flemming, Van Beneden and Strasburger.

By 1885, Hertwig and Strasburger suspected that nucleus may be the basis of heredity. *It was not until* 1902 *when Sutton pointed out the parallelism between Mendel's laws and chromosome behaviour during cell division that the actual seat of hereditary particles was surmised.* Immediately following this, the advances in the post mendelian era were rather rapid.

Selection as an art has long been practised by man. Conscious hybridisation could not be practised in the early days because the role of the sexes in reproduction was not understood. Sex in animals is a long known phenomenon but sex in plants came to be recognised far later. In 700 B.C. in Egypt and Assyria, artificial pollination of dates was known. Hybridisation in rice is said to have been practised in ancient China. However, systematic attempts on hybridisation were made in the 18th century only.

In 1676, Grew suggested that stamens are the males. In 1694, Camerarius showed with the aid of microscope that sex in mulberry, castor and maize was similar to that in animals. It was not realised till then that the male contributes equally to the hereditary characters in the progeny.

That *like begets like* is a long known phenomenon. Thus, for example, a rice plant gives rise to a rice plant only. Since many thousands of years some plants and animals are nearly the same without any change. The phenomenon of like-begets-like conserves the existing type ; but yet there is a phenomenon of *variation* which tries to alter the progeny. It may be said that man took advantage of both the phenomena to domesticate plants and animals to his advantage. Selecting fortuitous variants was the only chance for improvement. When the existence of sex in plants was known, attention was directed towards bringing together parents which showed large differences between them. In some cases, very widely differing parents were mated as in the mating of horse and the ass to produce mule. In the case of plants too, several such attempts were made to produce new types.

The first artificial hybridisation in plants was by Kolreuter in 1760. He hybridised two varieties of tobacco. The progeny from this cross was intermediate between the parents in respect of many characters. This was conclusive evidence to show that the pollen parent also influences the characters of the progenies. Kolreuter was followed by many workers in plant hybridisation. Knight (1759—1838), a horticulturist, produced new varieties by hybridisation. He was the first to make back-cross and he noticed segregation. As a clever horticulturist he produced new types by hybridisation. John Goss (1820) hybridised two types of peas—one with bluish seeds and the other with yellowish white seeds. In the first generation, the seeds were all yellowish white but in the second generation he found both types appearing. Gartner (1849) was a prize-winner for his work on the role of hybridisation in plant improvement. He made a large number of species crosses and noted that in the first generation the plants were all uniform but in second generation there was variation. In 1854, Naudin secured a prize from Paris academy for his work on plant hybridisation. He showed that the characters did not blend and that the parental types appeared in the second generation of a cross. He also made *reciprocal crosses* and proved the identity of the F_1s. He almost

hit upon the laws of heredity but failed to enunciate them because he did not count the progenies.

It may be said that researches on (1) variation and evolution (2) cell as a unit of structure and function and (3) hybridisation were progressing side by side and the stage was set by 1900 to realise the importance of Mendel's laws. Though these were first published in 1866, the biologists of the day did not realise the far-reaching importance of Mendel's findings.

3. **Mendelian Era.**—Mendel (1822—1884), an Austrian monk, worked on garden peas. He started experiments in 1857 and published his results in 1866. He made crosses between different varieties of peas and studied the progenies. Instead of taking the parents or the progenies as a unit for study, he studied individual characters, thus introducing a new concept that an organism is a composite of a large number of independently behaving unit characters. In 1900, DeVries, Correns and Tschermak independently discovered Mendel's work first published in an obscure journal. *Thus dawned the twentieth century with the birth of a new branch of Biological Science.* This rediscovery of Mendel's Laws of heredity gave guidance and stimulation to hordes of other plant breeders. The new subject attracted many workers and by 1934, it was computed that 10,155 publications on genetics alone were published. Details of Mendel's work are discussed in a later chapter.

Immediately following the rediscovery of Mendel's Laws, many principles underlying the inheritance of characters were investigated. In 1906, Bateson coined the term '*Genetics*' to cover all matters concerning the "*Physiology of heredity and variation.*" This science "*seeks to account for the resemblances and differences exhibited among organisms related by descent.*" "*Heredity is genetic continuity of germinal material between parents and offspring. Variation is difference whether in the expression of somatic characters or in the elements of the germinal substance exhibited among groups of organisms related by descent.*"

In 1902, Sutton drew pointed attention to the fact that the behaviour of mendelian factors in heredity and that of chromosomes were parallel. This is the first step in the unification of Cytology and Genetics into *Cyto-genetics.* Therefore heredity was studied not only by observations on the manifested characters but also by observations on chromosomal changes. Thus, the *chromosome theory of heredity* was established. Researches by Morgan and his followers not only confirmed this theory but revealed many other cytological and genetical phenomena. Bateson and Punnett (1906) reported a case of linkage, *i.e.*, in the F_2 of a cross the parental types were predominant and the recombined types were fewer. They assumed that the parental types of gametes multiplied more rapidly than the other. Morgan (1912) enunciated his *linkage theory* and showed that *the genes located on the same chromosome are linked.* Jannsens (1909) studied meiosis in detail and pointed out chiasmata which later formed the basis for explaining *crossing-over.* These researches proved beyond doubt that the chromosomes constitute the *physical basis of heredity.* By extensive and complicated researches, the relative position of various genetic factors on particular chromosomes were located and diagrammatic *chromosome maps* were drawn up for the fruit fly *Drosophila.*

Johannsen's *pure line theory* is an important pronouncement of this *era*. It established the conservative nature of the genes and their stability. It also indicated a new breeding technique for isolating and purifying desirable types from mixed populations.

Mutation is another important genetic phenomenon which was first discovered by DeVries (1901). Till then, it was assumed that variation is continuous but *DeVries pointed out that large and discontinuous jumps also arise occasionally and these play an important role in the evolution of new species.*

Plant breeders hoped that by the application of Mendelism, new selections with re-combined economic characters could be selected by hybridisation. Soon, they found that many of the characters of economic importance were not easy of analysis due to complex nature of inheritance.

Thus, it may be pointed out that (1) the chromosome theory, (2) linkage and crossing-over, (3) details of meiosis, (4) extended researches on the inheritance of characters in plants and animals, especially in *Drosophila*, (5) mutation and (6) pure line selection are some of the important problems that attracted the attention of the biologists immediately after 1900.

4. **Recent Advances.**—Mendel distinguished *phenotype* from *genotype*. Therefore attempts were made to correlate genetical behaviour with changes in the structure of chromosomes. Since the chromosomes are generally small, detailed observations are not possible. The discovery of *salivary gland chromosomes* by Hertz and Bauer (1933) and the studies of Painter (1934) made it possible to study the structure of chromosomes in great detail. Pairing between identical *chromomeres* and structural changes like inversion can now be visually observed on the salivary gland chromosomes.

The discovery by Muller & Stadler (1927) that *X-rays* could be used to increase considerably the very low spontaneous mutation rate is of great significance. Thus many mutations were produced and studied in the various laboratories.

Sterility in wide crosses has been overcome by the discovery by Blakeslee and Avery (1937) that *Colchicine* doubles the chromosome numbers. This alkaloid has been found to be specific in its action of doubling the number of chromosomes in plant cells.

Muller and Dobzhansky have found that ' scute ' genes when translocated to new positions behaved differently. This is termed *position effect*. In discussing the nature of the gene and its mode of action, the position effect is an important phenomenon. The gene not only reacts with the external environment but also with its immediate neighbours in bringing about the phenotypic effect. This has the support of Goldschmidt who hypothesises that the whole chromosome or even the entire chromosome complement behaves as a unit. He has even doubted the existence of individual genes. The *theory of genic balance* may clear the issues in days to come.

The gene is now believed to be a living protein molecule. It is autocatalytic and enzyme-like in action. The discovery by Stanley (1935) that the tobacco

virus is a large living protein molecule brings it nearer to a gene. We are yet far from knowing the chemical nature of the gene or its exact mode of action. But it has been found that to a great extent the expression of character by the gene is dependent on the chain of chemical reactions initiated by the gene. The recent discovery that the hereditary character " antennaless " in fly can be changed to " antenna " by feeding the flies with vitamin B-2 indicates that the gene for antenna could synthesise vitamin B-2 by itself for the expression of the character.

In the field of plant breeding, the *multiple factor* hypothesis showed that the economic characters are governed by a large number of factors. Fisher, Haldane, and Wright have introduced mathematical analysis of population trends. Evolutionary trends have been discussed and valuable conclusions have been reached by this process.

In the fields of plant breeding, there are a few who feel that the capacity of a breeder to select new plants from unselected bulk is an intuitive in-born ability to spot the progenitor of a new superior race. With the introduction of new field plot technique and appropriate methods of statistical analysis, it is now increasingly realised that with the aid of statistical technique valuable cultures can be selected even in the early stages of selection.

The older methods of genetical research have been joined with chemistry and statistics as a powerful combination to unfold the new interpretation of life. *With the rapid progress now made by this science, a new epoch in biology is arising.*

Chapter 2

REPRODUCTION

MULTIPLICATION IN PLANTS—THE FLOWER—SELF AND CROSS-POLLINATION—DEVELOPMENT OF STAMENS—DEVELOPMENT OF PISTIL—FERTILISATION—ASEXUAL REPRODUCTION—CELL DIVISIONS IN REPRODUCTION.

1. **Multiplication in plants.**—Plants multiply by either of two methods (1) by means of seeds that are produced by the *sexual* process, (2) by development of new individuals from vegetative parts or the *asexual* process. For the formation of a seed, special type of cells, the reproductive cells, which are termed *gametes* are necessary. The gametes are of male or female sex and the fusion of two gametes of opposite sex leads to the formation and development of a seed. The gametes are unicellular and microscopic and these are developed in special structures found in the flowers of plants. In the case of vegetative propagation a new plant is developed from a separated branch of the plant. A 'cutting' or a bud may be used to propagate the plant vegetatively. In this method of propagation the progenies form "the chips of the same block" and they are not considered as new generations. If, for example, a superior variety of sugarcane, such as Co. 419 is propagated by the planting of setts, the progenies behave exactly like their parents in their growth, tillering, flowering and other economic characters. In fact, the progenies may be considered as branches of their parents and they are identical with their parents in respect of all the inherited characters. The progenies which arise by the sowing of seeds behave differently. The two gametes may come from the same plant or from different plants. If they are from two different plants, they bring together the characters of the two plants from which the gametes had their respective origin. Consequently, the seeds may not truly represent the parent plant from which they are harvested. *Plants which are multiplied sexually vary while those produced asexually do not.*

Though many plants are capable of multiplication by both the methods, in agricultural practice one or the other method is usually adopted : sugarcane, several fruit trees, potato, sweet potato, betelvine, colocasia, yam, turmeric, pepper, ginger, cardamomum, plantain, grapes, etc., are vegetatively propagated while cereals, cotton and pulses are raised from seeds. Since these two propagation methods lead to different consequences in the progenies in respect of inheritance of characters, they are important in genetics.

2. **The Flower.**—Young plants grow and increase in size for some time and later they put forth flowers and form fruits and seeds. *Growth and increase in size connote vegetative phase of the plant while flowering connotes the onset of the sexual phase.* The length of vegetative phase may be short or long depending upon the particular species or race. ***Annuals*** like rice, ragi, etc., flower in the course of a few months after sowing. ***Biennials*** flower in the second year of their growth. There are others like the coconut, mango, orange, apple, etc., which flower 5 to 7 years after their planting. *The length*

of vegetative phase is not only an inherited character but it is also largely influenced by the environment.

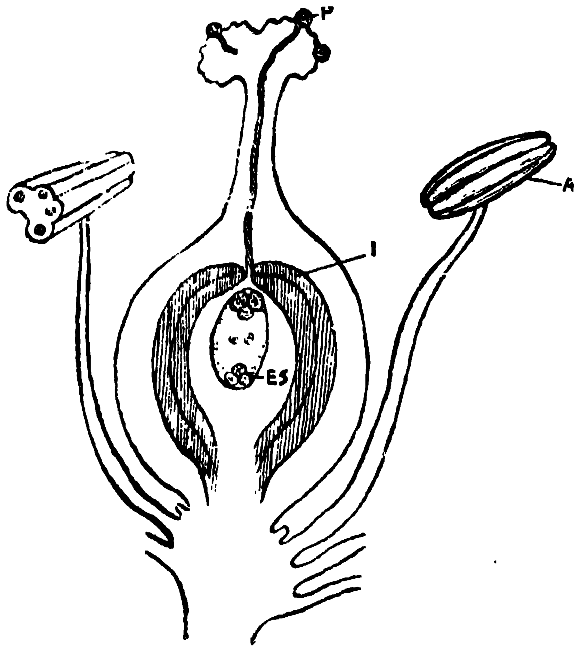

Fig. 1.—Essential parts of a flower. (P—pollen grain ; A—Anther sac ; I—integuments ; E.S.—Embryosac). The anther sac in cross-section is shown on the left side.

The male and female sexual organs which give rise to gametes of corresponding sex are borne in flowers. A typical flower is characterised by four whorls, (1) the Calyx, (2) the Corolla, (3) the Androecium, and (4) the Gynoecium, (Fig. 1). The calyx and the corolla are the outer whorls and they are accessory organs. The androecium and the gynoecium constitute the inner whorls and they are the essential sexual organs. The accessory organs are mainly for the protection of the essential organs in the early stages of flower formation and later, when the flower blooms, they play a great part in the mechanical contrivances which go to aid self or cross-pollination.

While all the four whorls are present in a typical flower, one or more of them may be absent in irregular and incomplete flowers. The calyx and corolla may be absent or considerably reduced or modified. When andrœcium is absent and gynœcium only is present, the flowers are termed *pistillate* ; when andrœcium only is present the flowers are termed *staminate*. In either case the flowers are *unisexual*. If staminate and pistillate flowers are borne on the same plant, the plants are termed *monœcious* and if on different plants *diœcious*. Generally when the flowers bloom the stamens and pistils are mature and are ready to function sexually. The pollen grains are shed on the stigma and this is termed *pollination*. The relative time of flower opening, maturation of stamens and pistil, and pollination may vary in different crops. The act of flowering is termed *anthesis*.

In the case of higher plants, the pollen grains are not motile by themselves. The pollen may be shed on the stigma of the same flower—*self-pollination* or *autogamy*. This is an easy process due to the nearness of the two organs concerned. There are many plants such as maize, cumbu, etc., where the pollen is usually transferred to the stigma of a different flower in another plant—*cross-pollination or allogamy*. Cross-pollination in plants is generally brought about through the agency of insects, water or wind. When the pollen grains of a flower fall on the stigma of another flower in the same plant, it is termed *geitenogamy* and genetically it is equivalent to self-pollination.

3. **Self and Cross-pollinations.**—Pollination may take place just at the time of flower opening or at varying periods before or after flower opening. When the anther sacs burst prior to flower opening, as in the case of beans, self-pollination is the rule. In some cases such as in rice, the pollination may take place simultaneously with or a short while after flower opening and in these plants self-pollination is most predominant.

In the case of diœcious plants cross-pollination is the rule. In monœcious plants such as maize and coconut, the scope for cross-pollination is greater though self-pollination is not ruled out. In the case of hermaphrodite or bi-sexual flowers there are various contrivances by which cross-pollination may be aided. The stamens and pistil may mature at different times (*dichogamy*) as in *Pennisetum typhoides*, thus enforcing cross-pollination. In this crop, the stigmatic branches emerge out first from the spikelets and the stamens emerge out and shed the pollen grains long after the stigma has lost its *receptivity*. This is termed *protogyny*. In most other cereals the stamens emerge out first from the spikelets and shed the pollen grains before the emergence of stigma and this is termed *protandry*. There are various other floral devices which bring about cross-pollination even in hermaphrodite flowers. In addition to such mechanical devices, there are some genetic and physiological causes that may prevent self-pollination and aid cross-pollination. For example, the stigmatic secretions may inhibit pollen tube growth down the style and thus prevent fertilisation. When this happens in the case of pollen and stigma of the same flower the latter is said to be *self-sterile* or *self-incompatible* ; if it is between pollen and stigma from different plants the latter are said to be *cross-sterile* or *cross-incompatible*.

In crop plants both self and cross-pollination may take place, and the relative proportion between the two may vary. For example, in rice, cholam and cotton, self-pollination is the prevailing type though cross-pollination in nature may take place in varying degrees. The two types of pollination lead to different genetic consequences in the progenies and therefore detailed studies on anthesis and pollination are important in genetical studies.

4. **Development of Stamens.**—The andrœcium or stamens represent *microsporophylls* or modified leaves bearing male spores or *microspores*. Stamens develop from the hypodermal tissues of the plant. A typical stamen consists of a *filament* bearing at its tip the *anther*. Each anther consists of two lobes and each lobe of two cavities (Fig. 2). These four cavities or sacs of a stamen represent *microsporangia* inside which the *microspores* or *pollen grains* are developed.

Anther development starts by the divisions in hypodermal layer. The first division is periclinal being parallel to the surface. The outer layer divides and forms the wall layers of anther, while the inner layer forms the *archesporial cells* or pollen mother cells (P.M.C.). Of the outer wall layers of the anther the first layer is the epidermis and the rest become thickened in their cell walls and are termed *fibrous layer*. The innermost layer is termed *tapetum* and this layer is full of protoplasm with prominent nuclei. This functions as the feeding layer to the archesporial tissue. Gradually tapetum disappears due to its contents being absorbed as food by the developing pollen grains.

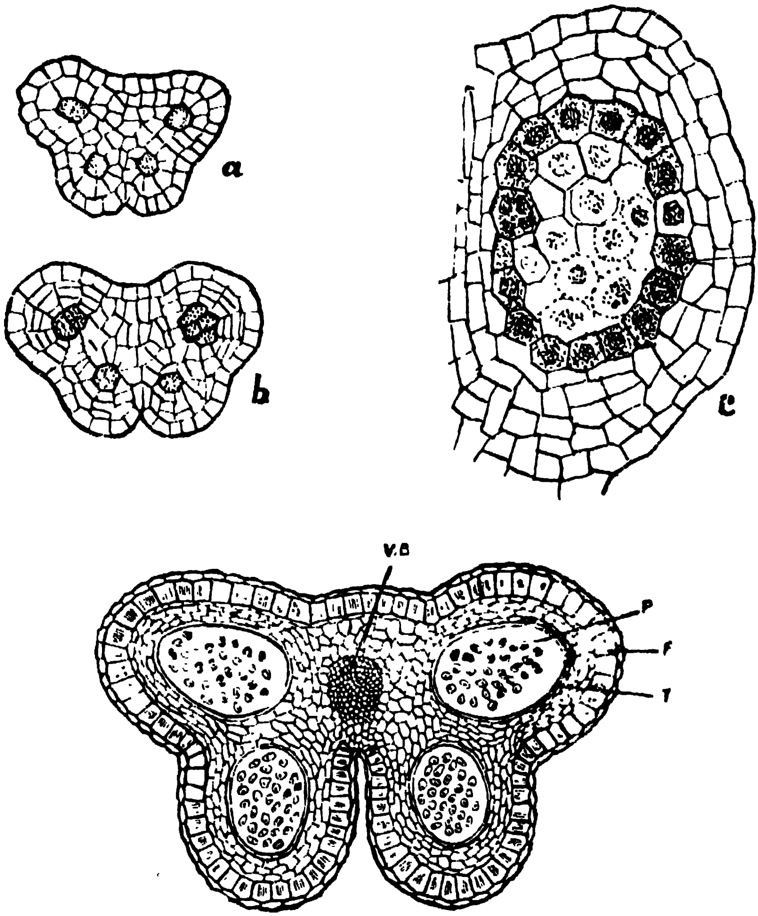

Fig. 2.—Stages in the development of anther sac, *a* and *b* initial stages. *c* : P.M.C. dividing. Note the tapetum with dense protoplasm. V.B. = Vascular bundle ; P = Pollen grains ; F = Fibrous layer.

The pollen mother cells undergo meiotic cell division or reduction division. The details of this cell division are discussed in Chapter V but it may be pointed out here that as a result of this division, each P.M.C. gives rise to four daughter cells and the chromosome number in each daughter cell is reduced to half the number found in any somatic cell of that plant. The first division of meiosis divides P.M.C. into two cells (dyads) and at the end of second division,

P.M.C. is divided into four cells (tetrads). In dicotyledonous plants cell wall formation may be delayed upto tetrad formation but in monocotyledonous plants cell wall formation may begin at the dyad stage. Each one of the four cells in the tetrad develops into a pollen grain. On account of the reduction division in the P.M.C. the nucleus in the pollen grain contains *n* chromosomes or *haploid* complement as compared to $2n$ chromosomes or *diploid* complement in the somatic cells.

When the pollen grains are fully developed in the anther sacs, the two chambers of the anther lobe coalesce into one and when the weather conditions are favourable, the cell wall of the anther bursts and the pollen grains are shed.

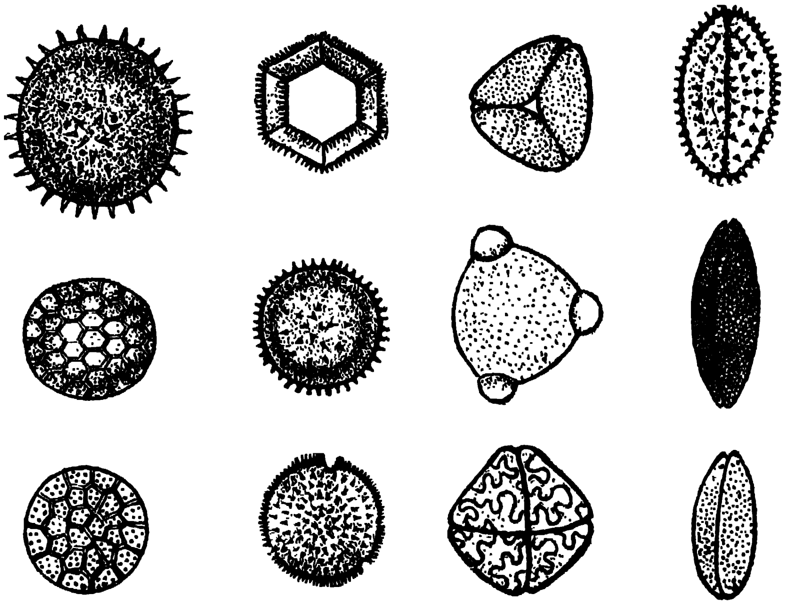

Fig. 3.—Different types of pollen grains. Note the markings on exine that are helpful in pollination and the emergence of pollen tube.

The pollen grain consists of thick cutinised outer covering termed *exine* and an inner thin cellulose layer termed *intine*. When the pollen grain is transferred to the stigma it germinates. The structure of the pollen grain and the various markings on the exine are adapted for pollination (Fig. 3).

There are various types of weak spots on exine through which the pollen tube emerges out. The wall of the pollen tube is continuous with the intine. The pollen tube penetrates the stigmatic tissues and grows down the style towards the ovules. When the pollen grain germinates two nuclei can be seen, (1) the *vegetative nucleus* (2) *the antheridial nucleus* which by a further division gives rise to two *generative nuclei* which constitute the microgametes (Fig. 4.).

5. **Development of Pistil.**—Pistil represents the *megasporophyll* and it develops from the hypodermal layers of the plant. The relative size and development of ovary, style and stigma vary in different plants. The ovary contains one or more *ovules* each containing a *megasporangium* (Fig. 5). The

carpels bearing the ovules may be variously united. The ovules are attached to fleshy margins of carpels (placenta) by means of stalks (funicles). The funicle is attached to the ovule at chalaza from where one or two integuments

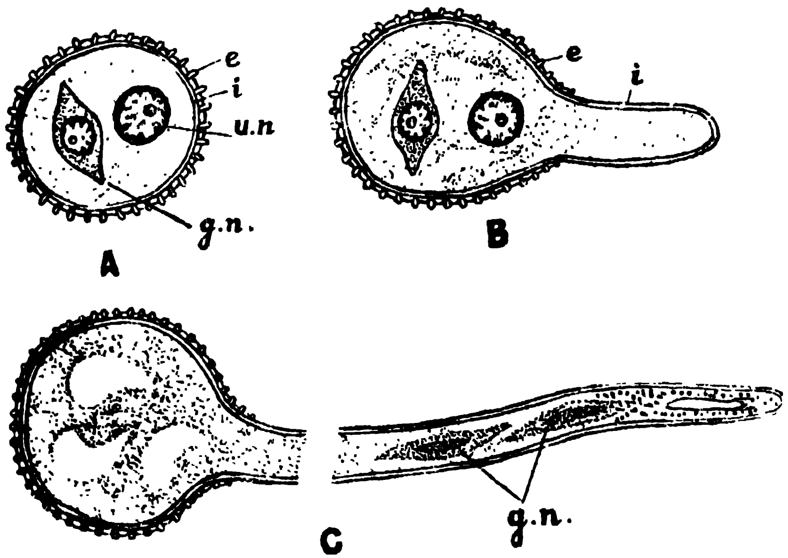

Fig. 4.—Pollen grain. A : parts of a pollen grain ; e=exine, i=intine, a.n.= antheridial nucleus, g.n.=generative nucleus. B : Pollen grain in germination. C : Pollen tube with the two generative nuclei.

arise and envelop a mass of tissue termed *nucellus* (the *megasporangium*). The integuments stop short of fusing at the top and leave a minute aperture, the *micropyle*. Beneath this micropyle the *megaspore* or *embryosac* is em-

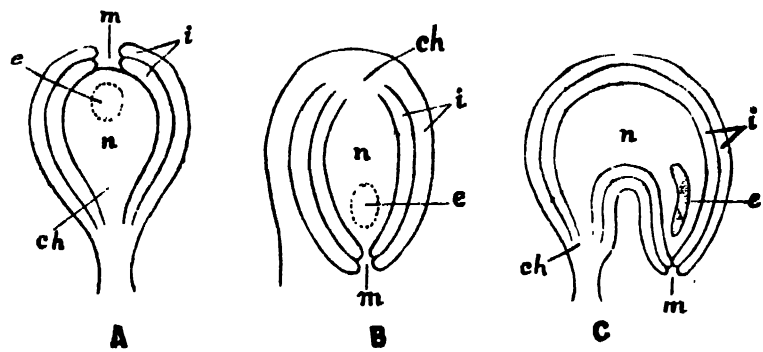

Fig. 5.—Ovules. A : Orthotropous, B : Anatropous, C : Campylotropous. m= micropyle, ch=chalaza, n=nucellus, e=embryo-sac.

bedded in the nucellus (Fig. 6). The embryosac is developed from one of the cells of nucellus. This single cell functions as the archesporial cell or egg mother cell (E.M.C.). This cell undergoes meiotic division or reduction division and forms a tetrad of four megaspores all of which contain haploid number of chromosomes. Out of the tetrad, three cells disintegrate and the last one develops into embryo-sac. The primary nucleus of embryosac divides thrice and forms eight nuclei. When the ovule is ready for fertilisation three of these are situated near the micropyle, three at the opposite end of the embryo sac and two at the centre.

The three nuclei at the micropylar end form naked *cells and are termed* the *egg-apparatus.* The two *lateral cells here form the synergids* and the middle one, the *mega-gamete.* The three nuclei at the opposite end are termed *antipodals.* The two nuclei at the centre of the embryo-sac constitute the *primary endosperm nucleus.* The foregoing is a brief description of the development of megaspore of normal type in angiosperms but 14 types of variations have been recorded.

6. **Fertilisation.**—When the pollen grain falls on the stigma at the time the latter is receptive, it is held on to it by means of secretions on the stigma. The pollen grain absorbs moisture from the stigma and swells up. Through the weak spots on exine, the inner protoplast enlarges and comes out in the form of a tube. This tube penetrates the stigma and style and grows down towards the ovules. The centre of the style may either be hollow or be filled with thin walled cells. These cells constitute the feeding layer for the growing pollen tube. The tube finally enters the ovary and reaches the ovule usually through

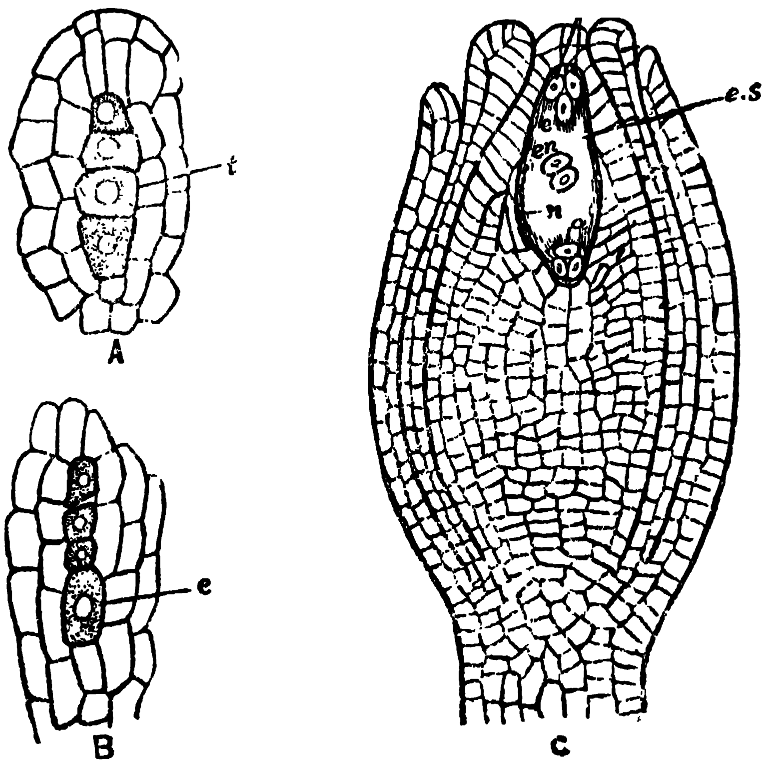

Fig. 6.—Ovule in development. A : initial stage showing tetrad. B : later stage showing only one cell of the tetrad enlarging. C : Final-stage showing embryo-sac. e.s.=Embryo sac, s=synergids, e=egg, *e.n.*=endosperm nucleus, a=antipodals. The embryo-sac is embedded in nucellus (n).

the micropyle. By now, the generative nucleus has divided into two microgametes. When the tip of the pollen tube enters the micropyle, it bursts and releases the two microgametes. *One of the microgametes fuses with the megagamete to form the Zygote and this fusion is termed syngamy or fertili-*

sation. The othei microgamete passes to the centre and fuses with the endosperm nucleus which is already a product of fusion of two nuclei. The zygote contains 2n chromosomes on account of the coming together of n chromosomes from each of the gametes, the male and the female. The endosperm contains 3n chromosomes two of which are from the embryo-sac and one from the microgamete. The remaining tissues of the ovule, *viz*., the nucellus and integuments as well as cells of the ovary contain 2n chromosomes of maternal origin. The act of fertilisation has introduced one haploid paternal complement in the formation of zygote and another similar paternal haploid complement in the formation of endosperm.

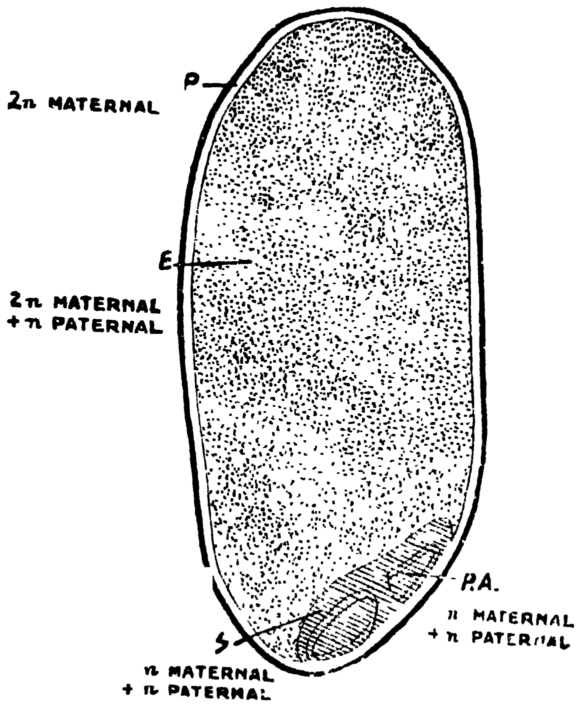

Fig. 7.—Diagram showing the chromosome number in different tissues of a seed. P = Seed coats which are maternal in origin with 2n chromosomes : E = Endosperm which is both maternal and paternal in origin with 2n maternal and n paternal chromosomes : S = Cotyledon and P Primary axis which contain n maternal and n paternal chromosomes, are developed from zygote.

After fertilisation, the ovary develops into fruit, the ovule into seed, the integument into seed coats, the zygote into cotyledons and primary axis, nucellus into perisperm and endosperm nucleus into endosperm. When two different types of plants are crossed, in the seed the embryo (cotyledons and primary axis) and endosperm are of hybrid genetic constitution while the remaining parts of the seed are maternal only in genotype (Fig. 7).

The megaspore is deep seated within the pistil and is surrounded by a mass of sterile maternal tissue. Therefore, if the sexual reproduction in plants

is to be successful, the following steps must be successfully completed : formation of functional gametes, successful pollination, germination of pollen grain, proper growth of pollen tube through the stigma and style and finally fertilisation and normal development of seeds. Failure at any one step leads to the failure of sexual mechanism. Even after fertilisation in the course of development of the zygote into functional seed, irregularities may occur which will result in failure of sexual reproduction.

7. **Asexual Reproduction.**—Certain crop plants such as sugarcane, sweet potato, plantain, potato, etc., are multiplied vegetatively. The group of plants derived from a single parental stock is termed *clone*. Vegetative propagation is resorted to sometimes by the agriculturists because (1) the crop may not produce seeds (2) when multiplied through seed, the crop may show wide variation and may not breed true to the parental type as it often happens in fruit trees such as mangoes and oranges, and (3) cultural practices in vogue may not be favourable for seed sowing.

Seed being the product of fusion of two sexual gametes, cross-pollination gives scope for Mendelian variations in the future generations. In vegetatively propagated plants, there is no scope for such variations. Even after many years of cultivation and vegetative propagation, the crop retains its original characters. It is mainly due to this reason that many of the fruit trees evolved many years ago and propagated vegetatively still retain the desirable characters. The thousands of trees of any choice fruit variety, such as for example 'Alphonso' in mango, are all vegetatively derived from a single selected tree In fact these progenies are as said before " chips of the old block."

The asexual propagation mentioned in the preceding para may consist in the planting of cuttings or propagation by budding and grafting. There are methods of vegetative propagation found in Nature which for all superficial purposes resemble sexual reproduction but lack in their essential steps such as reduction, division and fertilisation. This asexual phenomenon is termed *apomixis*. When the egg cell continues to grow without fertilisation it is termed *parthenogenesis*. There are two possibilities here : (1) if fertilisation fails and the egg develops into a plant the latter is haploid, (2) if meiosis fails in the formation of megaspore, the progeny will be diploid. In higher plants, the behaviour of polar nuclei is variable ; in some cases they fuse with the pollen nucleus even though fertilisation fails in the egg and in others fertilisation in polar nuclei may also fail.

In rare cases, the synergids, the antipodals, cells of integument or endosperm or more than one cell from the female tetrad may develop to form supernumerary embryos. This is termed *polyembryony*. This is very common in *Citrus* and less in mangoes. It is also rarely met with in crops like rice, cholam, ragi, etc. Out of many embryos formed, only one or none at all is the product of sexual process. The rest represent vegetative buds arising from the diploid tissues of the mother plant. For the development of adventitious embryos stimulation by pollination may be necessary. In some instances, even foreign pollen from a different species or genera may function to stimulate the unreduced egg to develop parthenogenetically and this false

sexual step is termed *pseudogamy*. If all the embryos in a case of polyembryony are of asexual origin, the seeds may be used to propagate the plant and the progenies are all true to the parent plant. This is found to be the case in some varieties of mango in which polyembryony is purely of vegetative origin.

8. **Cell Divisions in Reproduction.**—By repeated division of the zygote a new plant is developed. In the vegetatively propagated plant, new ones arise by the division of cells in the vegetative propagule. *Therefore division of pre-existing cells is a vital process in growth and development.* There is one vital difference between the sexual and asexual reproduction, *viz., in the sexual process at one stage, two cells each with half the normal chromosome complement fuse and restore the chromosome complement to the diploid level* (Fig. 8). Further divisions after the fusion of the haploid cells are the same

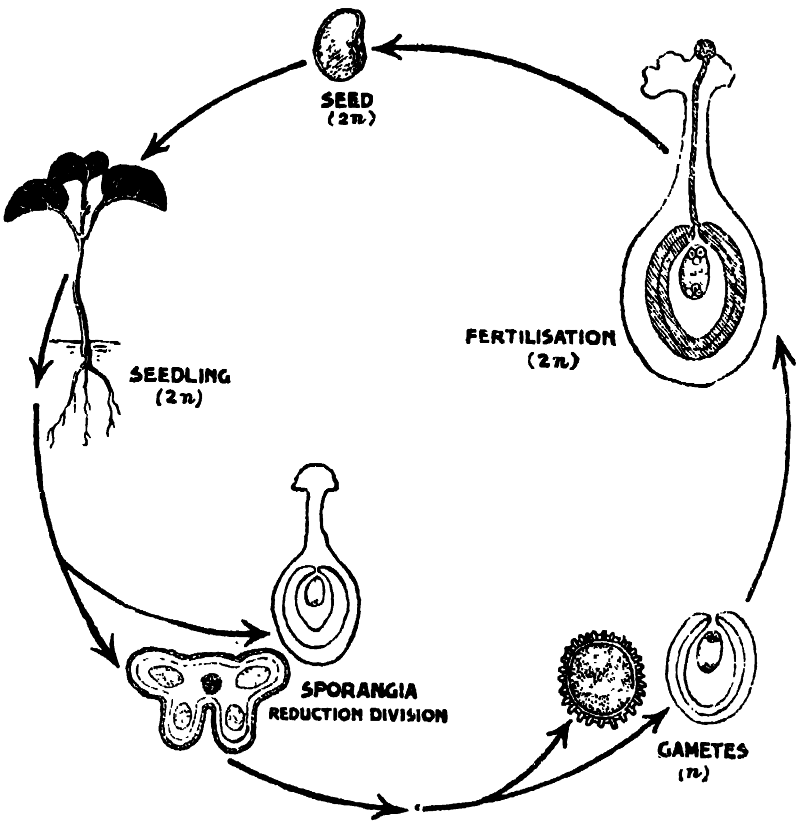

Fig. 8.—Diagram to show the life cycle of a crop plant and the stage at which reduction division and fertilisation take place.

as the cell divisions taking place in asexual propagation. Therefore there are two types of cell divisions (1) cell division leading to the formation of gametes with haploid chromosome complement and termed *meiosis* or *reduction division* (2) cell division that is normally taking place in all other cells and termed *mitosis.*

Reduction division is only a contrivance to maintain the same chromosome number of the species even after the fusion of two gametes. This reduction takes place once for every generation at the time of formation of gametes.

In the case of self-fertilisation in homozygous plants, the chromosome complements in the two gametes are identical in every respect. When two different varieties, races or species of plants are crossed, the two haploid chromosome complements are not identical but they differ in their genic contents and arrangements. The two complements remain together during the growth of the plant but when gametes are formed, exchange of genic materials between the paternal and maternal chromosomes takes place. This sort of exchange of genic materials between the chromosomes does not occur in mitosis. Since the genes are the carriers of hereditary characters from parents to progeny, *meiosis is the basic cause for the variations in the progenies from crosses.* In mitosis each chromosome divides longitudinally and the separation of the two halves results in the formation of two daughter cells without any change in the genic constitution or number of chromosomes . (*vide* Chapter V).

Chapter 3

SEGREGATION AND INDEPENDENT ASSORTMENT

SELECTION AS AN ART—CHARACTER PAIRS—MENDEL'S TECHNIQUE—3 : 1 RATIO—FACTORS IN GAMETES—SYMBOLS SEGREGATION—PHENOTYPE AND GENOTYPE—RECIPROCAL CROSS—BACK CROSS—DIHYBRIDS : 9 : 3 : 3 : 1 RATIO INDEPENDENT ASSORTMENT BACK-CROSS IN A DIHYBRID—PRACTICAL APPLICATION MENDEL'S GENIUS.

1. **Selection as an art.**—The art of selecting different types of crop plants and garden plants remained a matter of individual skill of the gardener. Prior to 1900, various workers tried hybridisation between different types of plants. The historical facts outlined in Chapter 1 brought out the various observations concerning the behaviour of hybrid progenies. Some of the predecessors of Mendel, notably John Goss and Naudin realised some orderliness behind the observed phenomena but they failed to discover laws of inheritance. Diverse facts were accumulated but the definite basis governing the same was not understood.

Many of the useful plants were brought under cultivation since pre-historic times and these were chosen because they possessed certain useful characters. Continued cultivation and selection of better types have been responsible for the evolution of cultivated plants and such plants showing useful characters, were developed under careful nurture. Other plants not cultivated by man underwent changes and continued to thrive under natural circumstances due to their possessing certain advantageous characters such as drought or disease resistance, hardiness, etc. The characters found in cultivated plants or wild plants have evolutionary background. Any character found in crop plants has had similar origin with the corresponding character found in other varieties or even in the wild ally.

2. **Character pairs.**—Characters are transmitted to the progenies from the parents through the medium of *factors* or *genes* which are located in linear order on the thread like structures, the *chromosomes*, in the *nucleus*. Hereditary differences between individuals, varieties, races, species, etc., arise by small or large changes in the genes. If we take for example, the blackish purple colour in the glume of cholam, a factor designated ' P ' is located on one of the chromosomes at a particular fixed point termed *locus*, and that ' P ' is responsible for the development of blackish purple glumes. For reasons which we shall not discuss now, the gene ' P ' changed with a corresponding change in the expression of the character from ' black ' to ' brown '. The changed gene is now designated as ' p '. The two characters *viz.*, blackish purple and brown, form a *contrasting pair* of characters and the genes P and p are termed *allelomorphs*. A cultivator identifies a particular variety of his crop by a group of characters present in that variety but absent or different in others. The greater the number of such contrasting pairs of characters the greater is the difference between the two varieties. *It must be noted that*

every character may have a contrasting character in another type. This character contrast is important in the study of inheritance because it can be traced in progenies of a cross.

3. **Mendel's technique.**—Mendel studied the inheritance of seven character pairs and laid the foundation for the new science of Genetics by enunciating laws of inheritance. He differed from his predecessors in the very conception of the problem. Till then two parents were chosen and crossed and the progeny was studied without reference to any particular character pair. All the characters of the parents were considered together as one unit with the result that the hybrid resembled the male parent in one set of characters and the female parent in another set and in later generations the phenomenon was more complex. *Mendel's success is due to the fact that he studied a single trait in the F_1 and further generations.*

Mendel was an Austrian monk of Brunswick. He was a mathematician and interested himself in hybridisation work on garden peas. He started his work in 1857. He obtained 34 varieties of garden peas which he raised for two years to see if the progenies showed the same characters as the parents year after year in which case the plants are considered to be true breeding. In genetical studies this is an important step. A character must be constant from generation to generation. Mendel chose garden peas because there were a large number of cultivated types which differed from each other in few character pairs only. From out of 34 varieties Mendel finally selected 22 varieties. He effected crosses between types differing in some character or other. In the end, he chose only 7 pairs of characters for his detailed study. In the hybrids and further generations he concerned himself with only one character pair at a time. *He considered the plant as a composite structure made up of a large number of unit characters.* Thus the hybrid (F_1), the second (F_2) and further generations (F_3, F_4, etc.) were studied with reference to the particular character pair in which the parents also differed. Thus, when he crossed a tall plant with a dwarf plant he found the hybrid tall and in F_2 generation there appeared both tall and dwarf types. There were few other characters in which the parents and the progenies showed contrast, but Mendel did not study them all conjointly with the character pair tallness--dwarfness.

Mendel counted the number of tall and dwarf plants in F_2. He picked the seeds of the F_2 plants individually and sowed them and again counted the tall and dwarf plants in F_3 of different F_2 plants. Thus he maintained pedigree records for every one of the plants and counted the progenies falling into different character groups such as tall dwarf. *The introduction of simple mathematics, viz., counting, was greatly responsible for rendering inheritance in terms of ratios. The simplifications of the problem by studying the progenies of a cross, character by character, maintenance of pedigree records and counting different types in the second and third generations are the chief points that enabled Mendel to understand and enunciate clearly the laws of heredity.* When Mendel crossed a tall plant with a dwarf one, the hybrid (F_1) was tall. In F_2 generation, both tall and dwarf plants appeared in a definite proportion. This shows that the factor for dwarf character co-existed with that for tallness in

F_1 generation. *Though the two factors, viz., factors for tallness and dwarfness are present in the hybrid, only the factor for tallness expresses itself while the factor for dwarfness does not. Therefore tallness is said to be* **dominant** *over dwarfness and dwarfness is said to be* **recessive** *to tallness.*

Mendel studied the following 7 pairs of characters and his data are summarised below :—

TABLE 1.

Character pair.	Character of hybrid *i.e.* dominant character.	In F_2 Population. Dominant.	In F_2 Population. Recessisve.	Proportion of Dominant : Recessive in F_2.
1. Smooth *vs.* wrinkled seed form.	Smooth	5,474	1,850	2·99 : 1·01
2. Yellow *vs.* green cotyledon	Yellow	6,022	2,001	3·00 : 1·00
3. Coloured *vs.* white seed coat.	Coloured	705	224	3·04 : 0·96
4. Hard *vs.* soft pod type ...	Hard	882	299	2·99 : 1·01
5. Green *vs.* yellow pod colour.	Green	428	152	2·95 : 1·05
6. Axial *vs.* terminal flower position.	Axial	651	207	3·03 : 0·97
7. Tall *vs.* dwarf state ...	Tall	787	277	2·96 : 1·04
Total ...	...	14,949	5,010	3·00 : 1·00

The contrasting pairs of characters, tallness Vs. dwarfness, etc., are termed " differentiating characters " by Mendel. That all the characters in animals and plants form such pairs has been borne out by many later experiments.

3 : 1 Ratio.—Following the re-publication of Mendel's work in 1900, Mendel's principles were tested on varied crops all over the world. Bateson showed that the same principles apply to animals as well as plants. The same phenomenon may be explained by taking the glume colour of the spikelets in *Sorghum*. The sessile spikelet in Sorghum shows the following structure : two glumes which are infertile, lower lemma usually epaleate and sterile, the upper lemma and its palea enclose 3 stamens, a pistil and a pair of lodicules. When the grain matures it is still enclosed between upper lemma and its palea. These two, in common parlance, are also termed as glumes and the inheritance of colour of the glumes is taken here as an example.

A cholam type with blackish purple glume was crossed with another type with brown glume. The F_1 plant developed blackish purple glume showing that to be dominant. The F_1 plants were selfed and the seeds sown to raise F_2 generation.

Both the dominant and the recessive characters appeared in the ratio of approximately 3 blackish purple glume to 1 brown glume. All F_1 plants were uniform in appearance, while F_2 plants showed variations. The glume

types in F_2 resembled those of grand parents. In F_1 generation the factors for the two types of glume colour co-existed and in F_2 generation when the grand parental types appeared there were no signs of change in the glume colour.

5. **Factors in Gametes.**—In all cases of sexual reproduction, the progeny arises by the fusion of the two gametes *i.e.* the male (♂) and the female (♀). *The gametes form the physical link between the parents and the progenies.* So all characters of the parents are transmitted to the progeny through the gametes only. The gametes are microscopic and unicellular each carrying a prominent nucleus. Mendel, in the examples worked out by him assumed that there were "*somethings*" in the gametes which represented these characters and which were capable of visibly expressing or developing the characters concerned at the appropriate time. Later experiments most decisively proved the physical existence of this '*something*' or '*factor*,' termed the '*gene*.' Since the first vegetative cell is formed by the fusion of two unicellular gametes resulting in zygote it contains the factors in duplicate or *diploid number*, while the gametes contain the same in single or *haploid number*. These factors or genes are now known to be located on the threadlike bodies or chromosomes which are the important constituents of nuclei. In all the species, races or types, the chromosome number is fixed. In the somatic cells there are two sets of chromosomes—one from the male and the other from the female parent. When the two complements are identical, which is the case in plants self-fertilised over a number of generations, the plant is said to be *homozygous*. When two complements differ in respect of any factor pair, the plant is said to be *heterozygous* for that factor pair. Naturally-cross-fertilised plants are generally heterozygous for many factor pairs.

6. **Symbols.**—To trace the factors or genes from generation to generation they are symbolised. In the allelomorphic pair purple and brown glumes, purple is dominant over brown. Generally the first letter of the dominant character is taken to symbolise the factor. The two members of the allelomorphic pair of factors have similar evolutionary back-ground. Therefore one of the pair is represented by capital letter and the other by the corresponding small letter. The dominant character is always represented by capital letter and the recessive by lower case letter.

In the homozygous parents, the factors, are present in diploid number, *i.e.* *PP* or *pp*. The gametes contain them in haploid number, *i.e.* *P* or *p*. It follows therefore that all the gametes of the homozygous purple glumed parent bear only P, and those of brown parent bear only *p*. When these two types of parents are crossed these two factors P and p are necessarily brought together in the zygote through the respective gametes and therefore the diploid constitution of the hybrid will be *Pp* and this type is termed *heterozygous*.

7. **Segregation.**—In the example considered under section 4, the parents are symbolised as follows :—

Blackish purple	PP.
Brownish	pp.

(The dominant type is symbolised by capital letters and the recessive by lower case letters.)

In the generations following the cross, the factors may be traced as shown below :—

Parents :	Blackish purple PP	Brownish pp
Hybrid (F_1) :	Blackish purple Pp	
Gametes from F_1 :	P and p.	

In the foregoing symbolisation the following points are to be noted :

Parents are diploids and hence the somatic cells bear the factors in duplicate. Since the parents are homozygous as shown by breeding tests prior to crossing, the two factors in any cell are of the same kind (PP or pp). The gametes are haploids and hence they obviously contain only one member of the allelomorph (P or p only). In respect of any factor pair, the gametes are always pure. The F_1 appears blackish purple but contains both the factors Pp. It is therefore heterozygous or in other words results from the fusion of two dissimilar gametes. As purity of gametes is the law, the gametes formed by F_1 are also pure in respect of any factor pair as in the case of the gametes of the parents, *i.e.*, they carry P or p. The gametes of F_1 differ from those of the parents in that there are two kinds—(1) those bearing P (2) those bearing p, while the gametes of any one parent are all of one kind only, *i.e.*, either P or p. The two kinds of gametes in F_1 occur in equal proportion in both the sexes and they unite at random. During the formation of gametes, pollen mother cell or egg mother cell undergoes reduction division and it will be shown in a later section that out of every factor pair one member goes to one pole and the other goes to the opposite pole and because of this phenomenon the two members of a factor pair get separated or *segregate* and also they occur in equal frequencies. The male and female gametes of F_1 unite at random and as a result the two types of male gametes and the two types of female gametes give rise to 4 possible gametic combinations as shown in the *checker board.* (Fig. 9).

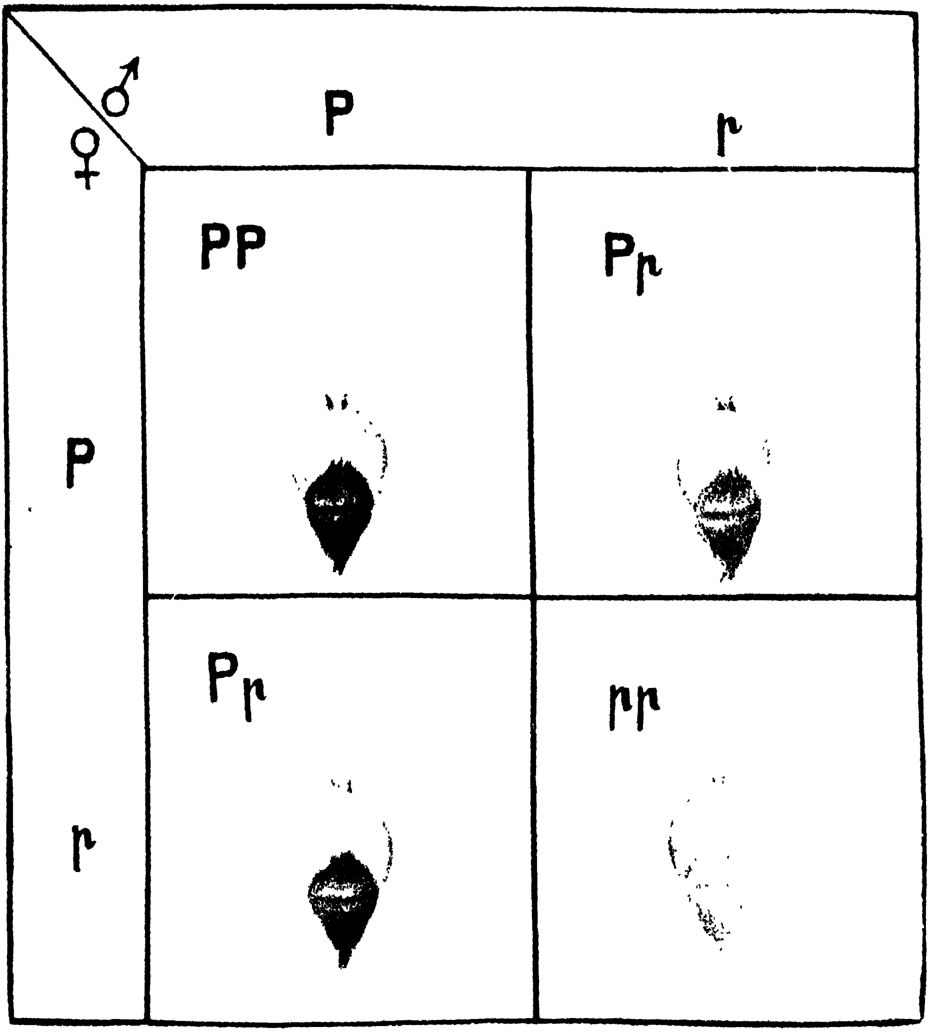

Fig. 9. Monohybrid. 3 : 1 Ratio.

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Thus it is seen that the factors P, p, which were brought together by hybridisation and which co-existed for the full vegetative life period of the plant separate out in the gametes when the plants mature. This is termed *segregation* of factors. That the factors segregate in the different gametes

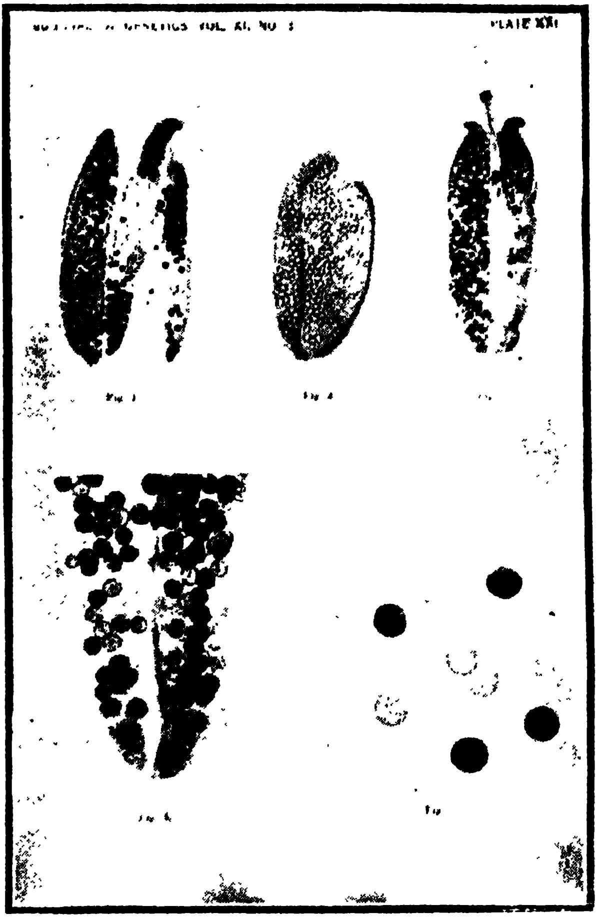

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Fig. 10 Iodine reaction of starch in pollen grains. (1) Anther of *starchy* type, pollen all dark (2) Anther of *glutinous* type, pollen all light (3) Anther of F1 pollen mixture of dark and light (4) Part of F1 anther more highly magnified (5) Free pollen of F1 showing two types.

can be demonstrated visibly in the case of pollen dimorphism in the F_1 of a cross between starchy and glutinous rices. Iodine stains the endosperm of starchy grains deep blue whereas the endosperm of glutinous grains are stained reddish to dark brown depending upon the strength of the solution. The

and sister are mated. If the F_1 is crossed to any one of the parents it is termed *back-crossing*. Thus $Pp \times PP$ or $Pp \times pp$ constitutes back-crossing. In the former type all the back-cross progenies show the dominant character while in the latter, the dominant and the recessive appear in 1 : 1 ratio.

F_1	:	Blackish purple ; Pp		
Gametes of F_1	:	P and p		
Back-cross parent	:	Brownish, pp		
Gametes of B. C. parent	:	p		
Back-cross	:	Pp	×	pp
Back-cross progenies	:	Blackish purple	:	Brownish
		Pp		pp
Back-cross ratio	:	1	:	1

When the back cross parent is of recessive type, the progenies appear in equal numbers for the dominant and recessive character. The recessive parent gives rise to only one type of gametes, *viz.*, all with factor p only. Therefore, the segregation noted here, as well as the proportion in which the two types of progenies occur must arise from the F_1 gametes. That the F_1 gives rise to two types of gametes has been already shown and the back-cross shows that they occur in equal numbers. Back crossing is therefore useful in testing gametic proportion in F_1.

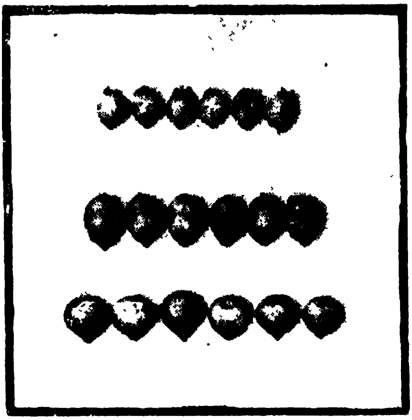
11. **Dihybrids (9 : 3 : 3 : 1 ratio).** After investigating the principles underlying the inheritance of a single pair of characters, Mendel considered a case of 2 pairs of characters, *e.g.*, smooth *Vs.* wrinkled seed form and yellow Vs. green cotyledon. The former set pertains to the seed form and the latter to colour of cotyledon. The proportion of different classes of seeds observed in F_2 is given below :

TABLE 2.

	Observed frequencies.	Expected frequencies on 9 : 3 : 3 : 1 ratio.
Smooth yellow seeds	315	313
Smooth green seeds	108	104
Wrinkled yellow seeds	101	104
Wrinkled green seeds	32	35

When any character pair is considered by itself such as smooth Vs. wrinkled, it is seen that the proportion of dominant to recessive is 3 : 1 and within each group again, the other character pair, *viz.*, yellow Vs. green cotyledon, shows a proportion of 3 dominant : 1 recessive. The four classes of phenotypes mentioned above therefore occur in the proportion (3 : 1) × (3 : 1) and the

expected frequencies are also shown above. Therefore it is evident that the mode of inheritance of two pairs of characters is similar to the monohybrid ratio. The following is an example from cholam The two pairs of characters



(*Photo from Millets Specialist*).

Fig. 12.—Cholam grains. Top row: Umbonate shape, Bottom row: Round top; middle row: The shape of F_1, hybrid.

considered here are (1) Pink Vs. White colour of grain and (2) Umbonate Vs. Round shape of grain. When grain shape alone was studied, umbonate shape of grain was dominant over round shape and in F_2, 328 umbonate : 121 round grains were observed. This is a close approximation to 3 : 1 ratio. In the case of grain colour, pink was dominant over white and in F_2, 278 pink : 82 white grains were observed. This is also a close approximation to 3 : 1 ratio When the four classes of phenotypes were studied in a segregating F_2 family, the following frequencies were observed.

TABLE 3.

		Observed frequencies.	Expected frequencies on 9 : 3 : 3 : 1 ratio.
Umbonate shape pink colour	...	279	284
Umbonate shape white colour	..	79	94
Round shape pink colour	..	116	94
Round shape white colour	...	29	31

In the total population, both the pairs of characters, *viz.*, shape and colour of grain show the normal segregation. When two pairs of characters are studied, there is no disturbance in the segregation of any one pair. Which-

ever pair of characters is considered, the other pair also shows normal segregation as represented below:

Umbonate shape	3 ...	Pink colour	3
		White colour	1
Round shape	1 ...	Pink colour	3
		White colour	1

In accordance with the expansion of the formula (3 : 1) × (3 : 1), representing the segregation of two pairs of factors, the F_2 population of a dihybrid shows 9/16 double dominant : 3/16 dominant—recessive : 3/16 recessive—dominant : 1/16 double recessive.

12. **Independent Assortment.**—The F_1 plant on maturing forms gametes and in the process the factors segregate as explained under section 7 of this chapter. Two pairs of factors segregate to form four types of gametes.

In the example considered above, the genotypic constitution of the parents and F_1 may be symbolised as follows :—

Parents	Kafir	and	Milo
Phonotype	Umbonate shape white colour		Round shape pink colour
Genotype	**UUww**		**uuWW**
F_1 : phenotype	Umbonate Pink		
F_1 : genotype	**UuWw**		
F_1 : gametes.	**UW, Uw, uW, uw**		

A gamete with factor U may also carry factor W or w and similar is the case with the gamete carrying u. As a result of random union between the male and female gametes, there are 16 gametic combinations as shown in the checker board (Fig. 13).

The results of the checker board may be summarised as shown below :—

TABLE 4.

Phenotype.	Frequency.	Genotype.	Frequency.	F_3 behaviour.
Umbonate pink ...	9	UUWW	1	Breeds pure.
		UUWw	2	Segregates in 3 : 1 ratio for grain colour only.
		UuWW	2	Segregates in 3 : 1 ratio for grain shape only.
		UuWw	4	Segregates for both the character pairs like F_1.
Umbonate while ...	3	UUww	1	Breeds pure.
		Uuww	2	Segregates in 3 : 1 ratio for grain shape only.
Round Pink ...	3	uuWW	1	Breeds pure.
		uuWw	2	Segregates in 3 : 1 ratio for grain colour only.
Round white ...	1	uuww	1	Breeds pure.

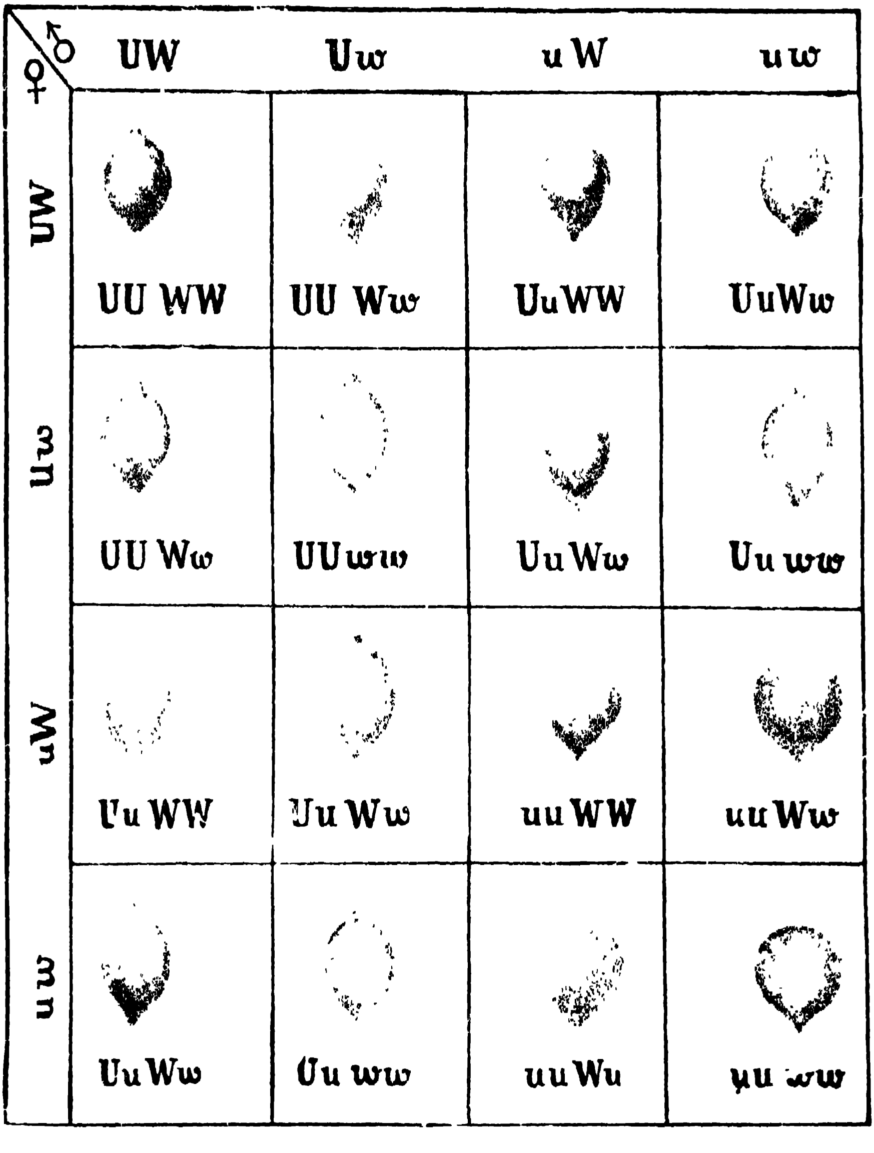


Fig. 13. DIHYBRID 9 : 3 : 3 : 1 Ratio. Note that the segregation for shape of grain is independent of segregation for colour of grain.

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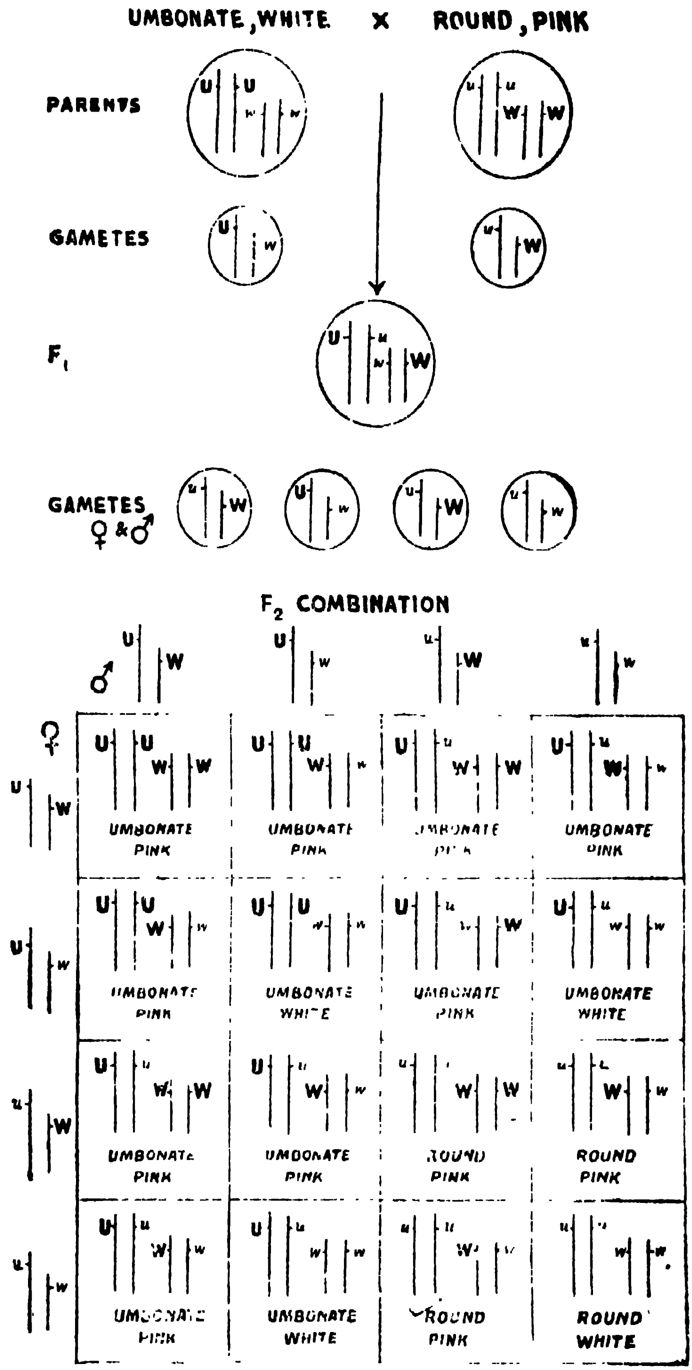

Fig. 14.—Diagram to explain segregation and independent assortment of factors as located on chromosomes. Note that when the gametes are formed, the chromosome with factor U goes along with the other chromosome carrying factor w or W. The homologues never enter the same gamete. This results in the formation of *four types* of gametes by the F_1 plants, and 9 : 3 : 3 : 1 ratio in F_2.

In F_2 segregation of a dihybrid there are four phenotypes but nine genotypes. *The different factors in a somatic cell assort themselves independent of each other when maturation division takes place to form gametes but the members of an allelomorphic pair always segregate into different gametes. This is Mendel's law of independent assortment.*

As in the case of monohybrid ratio mentioned under section 7, the independent assortment of factors may be demonstrated by observations on chromosomes during the formation of the gametes. Suppose that the two pairs of allelomorphic factors are situated on two pairs of chromosomes, the chromosomes and the factors may be traced through F_1 and F_2 generations as represented in Fig. 14.

The gametic combinations may be worked out by using the symbols and chromosomes in the checker board.

13. **Back-cross in a dihybrid.** The data obtained in F_2 population require confirmation. F_3 population may be raised and the breeding behaviour of the different F_2 families must conform to expectation as shown under section 12. The F_1 plant may be back-crossed to the double recessive parent in which case the following results are to be expected. (Table 5).

TABLE 5.

Back-cross progenies.	Umbonate pink.	Umbonate white	Round pink.	Round white.
Genotype	UuWw	Uuww	uuWw	uuww
Frequency	1	1	1	1

The four possible phenotypes occur in equal proportions and this results from the expansion of the formula (1 : 1) (1 : 1), a combination of two monohybrid back cross results. The double recessive parent being homozygous, forms only one type of gametes, *viz.*, uw ; therefore the different genotypes appearing in the back cross indicate the differences in the gametes of the F_1 plant. As already pointed out *back-cross is a means to test the gametic proportions in F_1.*

14. **Practical application.** The principles of segregation and independent assortment are of great practical significance. A review of the F_2 populations under section 12 reveals that in addition to the parental types, two more new types have appeared. The latter constitute the *recombination* of parental characters, and in the above example, the recombined forms are ' umbonate pink ' and ' round white '. *Thus by hybridisation a breeder is enabled to produce new types which do not occur in nature.* This is due to segregation and independent assortment of factors in F_2 and later generations. It was this possibility of creating new types that gave high hopes to plant breeders when first Mendel's laws were republished in 1900.

15. **Mendel's genius.**—The basic principles expounded by Mendel have been set forth in the preceding pages. Mendel worked with the garden peas but different examples have been cited above. Mendel's work formed the very basis for the modern genetics and plant breeding and it will be of interest to review here the few factors responsible for the success of Mendel in a field of work where great many other scientists had failed.

At the outset, the clarity of thought, simplification of the problem and bold thinking must be mentioned. Instead of considering the whole plant as a unit, Mendel considered character by character thus introducing a new conception that the plant is a composite of large number of independent and separable units of characters. Mendel maintained pedigree records of individual plants raised by him and counted the progenies in F_2 falling into different groups. Thus, for the first time mathematics finds introduction into plant breeding problems. It is of interest to note that Mendel himself was a keen student of mathematics. The choice of material, *viz.*, the garden pea, is a happy one because it is self-fertilised and there were many distinct cultivated types which differed from one another in a few characters only. Starting from the spade work done by his predecessors, Mendel enunciated the fundamental principles of inheritance of characters which are applicable both to plants and animals.

Chapter 4

MODIFICATIONS OF F_2 RATIOS AND DOMINANCE

MODIFICATION IN DOMINANCE—INTERACTION BETWEEN DOMINANT FACTORS—COMPLEMENTARY FACTORS—SUPPLEMENTARY FACTORS—EPISTASIS—INHIBITORY FACTOR—DUPLICATE FACTORS—POLYMERISM—MODIFICATIONS DUE TO INCOMPLETE DOMINANCE—LETHAL FACTORS—MOSAIC EXPRESSION—VARIABLE DOMINANCE—CYTOPLASMIC EFFECT—ENDOSPERM CHARACTER—XENIA—HETEROSIS—GENE SYMBOLS.

1. **Modification in dominance.**—In the seven pairs of characters studied by Mendel dominance was complete. In the F_2 generation, the homozygous dominant type and the heterozygous type phenotypically resemble each other and hence they cannot be distinguished and separated. In the preceding chapter under section 7 it was pointed out that blackish purple is dominant over brown in the case of glume colour in cholam. In the F_2 generation these two glume colours appear in the proportion of 3 blackish purple to 1 brown. The three blackish purple comprise of two genotypes PP and Pp. This genotypic difference is recognisable by carrying the plants to F_3 generation when it will be seen that the genotype PP breeds true to blackish purple glume while the genotype Pp segregates into 3 blackish purple : 1 brown as in the case of F_1 plant. The hybrid plant closely resembles the dominant parent in cases when dominance is complete.

There are instances where dominance is not complete. For example, in rice there are varieties with short or long outer glumes. T. 1083 with short outer glumes was crossed with F. B. 141 which has long outer glumes. The F_1 was intermediate between the parents in the size of the outer glumes.

The intermediate nature of the heterozygote is evidenced in the F_2 plants also. In actual field counts in this cross the following data were obtained in F_2 population.

TABLE 6.

Short outer glume.	Intermediate type.	Long outer glume.
436	808	412

The character is therefore monogenic with incomplete dominance.

2. **Interaction between dominant factors.**—In the case of the dihybrid considered under section 11 of the preceding chapter, the two factor pairs U-u and W-w controlled shape and colour of cholam grain respectively. The two pairs of factors pertain to two different traits of the grain. There are instances where the two pairs of factors may affect the same trait in different manner. An instance of this type was explained by Bateson and Punnett in the case of comb types in fowls.

There are four types of combs in fowls, (1) rose, (2) pea, (3) single and (4) walnut (Fig. 15). The comb type 'rose' is monogenic dominant to 'single'

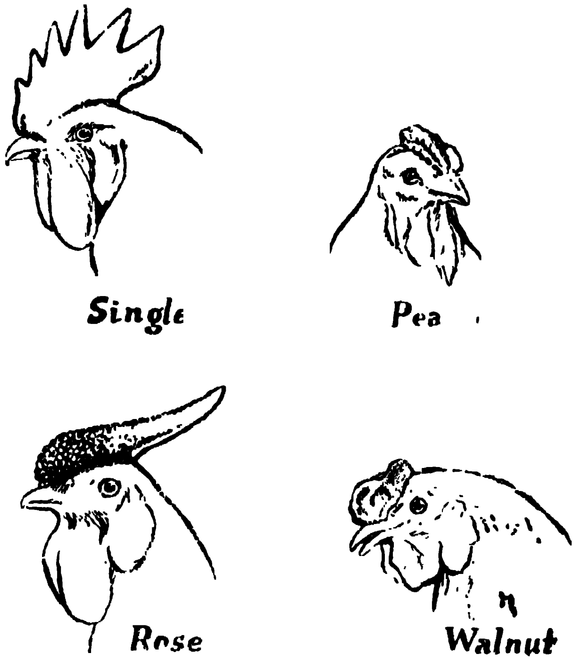

Fig. 15.—Types of combs in fowls.

and the factor pair is symbolised R-r. Similarly the comb type 'pea' is monogenic dominant to single and the factor pair is symbolised P-p. When 'rose' and 'pea' are crossed, the effect is that the two dominant factors R and P are brought together. Individually they have been found to produce two different types of combs and therefore it is not possible for the two factors to produce two different comb types in the same fowl. The two dominant factors interact and produce a new type of comb termed 'walnut'. This phenomenon is explained by the following factorial symbolisation.

Rose : ppRR
Pea : PPrr
Single : pprr.

ROSE × SINGLE.—(ppRR × pprr). The parents differ in a single pair of factors *viz.*, R-r. Therefore F_2 segregation shows 3 rose : 1 single.

PEA × SINGLE.—(PPrr × pprr). The parents differ in a single pair of factors, *viz.*, P-p. Therefore F_2 segregation shows 3 pea : 1 single.

ROSE × PEA.—(RRpp × PPrr). The parents differ in two pairs of factors. The F_1 genotype is Pp Rr and the dominant factors P and R interact to produce a new character, *viz.*, walnut. In F_2, both the pairs of factors segregate and the possible gametic combinations are shown in the checker board, Fig. 16.

The F_2 data may be summarised as follows :—

TABLE 7.

Phenotype.	Frequency.	Genotype.	Frequency.	F_3 behaviour.
Walnut . .		PPRR		Breeds pure.
		PPRr		Segregates into 3 walnut 1 Pea.
		Pp RR		Segregates into 3 walnut : 1 Rose.
		PpRr		Segregates like F_1.
Rose ..		ppRR		Breeds pure.
		ppRr		Segregates into 3 Rose : 1 single.
Pea ...		PPrr		Breeds pure.
		Pprr		Segregates into 3 Pea : 1 single.
Single ...		pprr		Breeds pure.

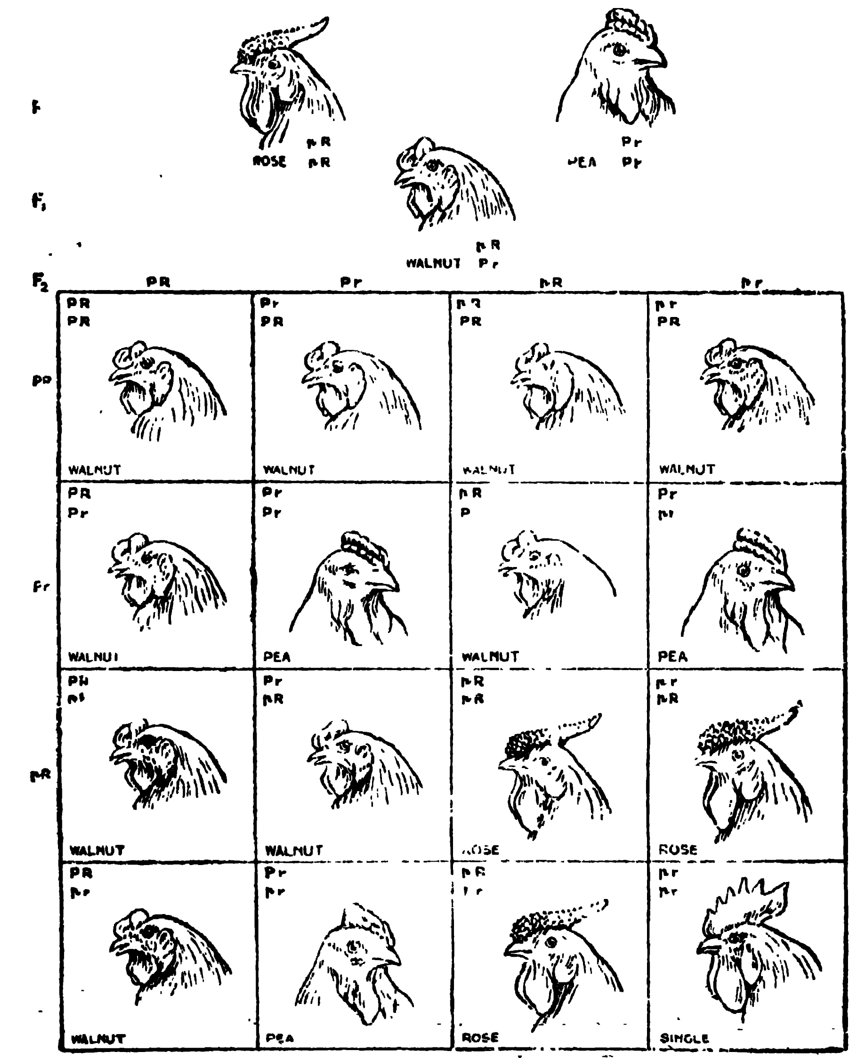

Fig. 16.— Diagram to bring out interaction between two factors. The factors P and R interact to produce the phenotype walnut.

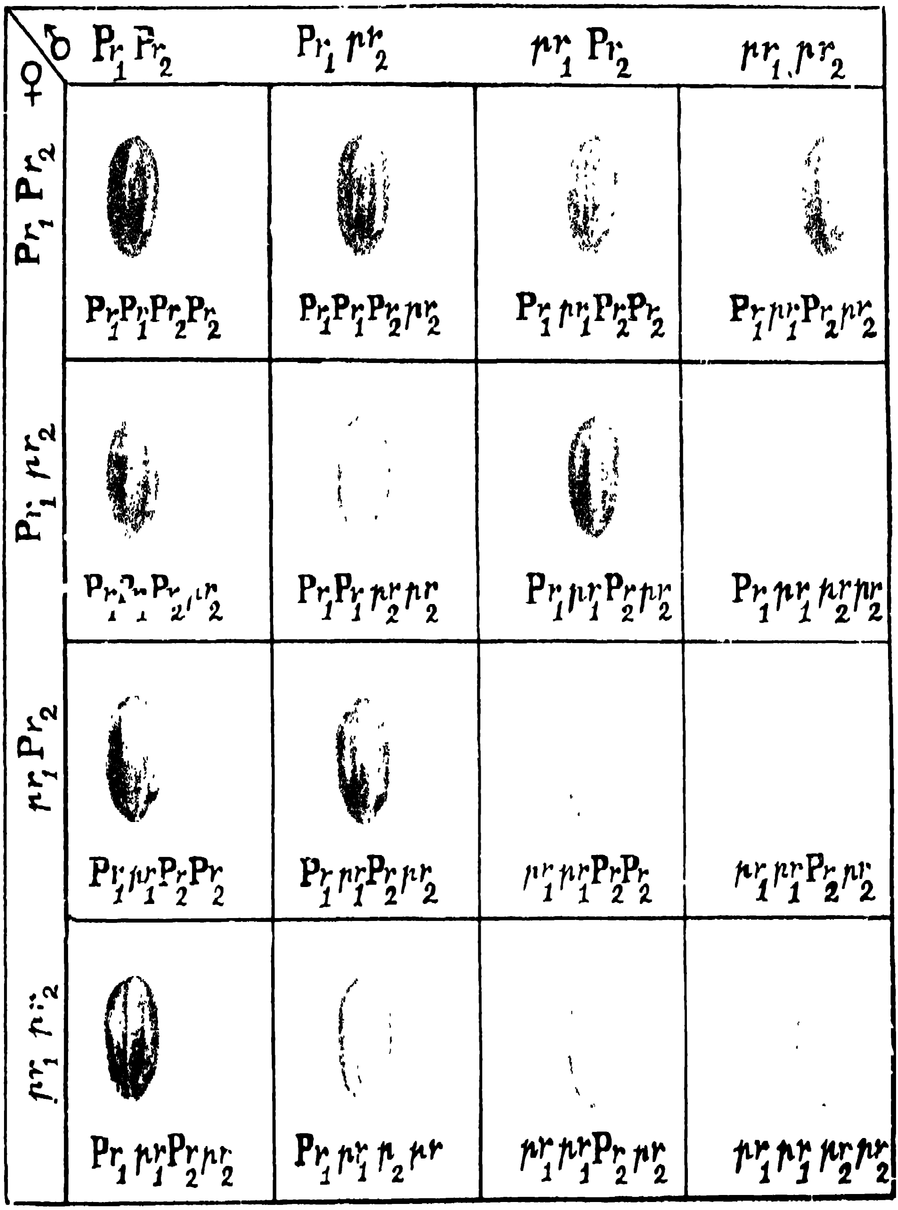

Fig. 17. Complementary Factors (9 : 7 Ratio).

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In the genetical analysis of the characters in crop plants instances of interaction between factors are frequent. In the grain colour of *Panicum miliaceum*, two factors L and O interact and produce four types of colours as shown below :—

	Interacting factors.
Light olive grey	LO
Dark olive grey	lO
Light buff yellow	Lo
Buff yellow	lo

3. **Complementary factors (9 : 7 ratio).**—Bateson and Punnett came across an instance in sweet pea where two different varieties having white flowers, when crossed gave hybrid plants with coloured flowers and in F_2 9 coloured : 7 white flowered types appeared. Similar instances were met with in many other plants. For example, in rice two grey grained varieties resulted in F_1 plants with red grains. In the segregating family 949 red grained and 753 grey grained plants appeared which is an approximation to 9 : 7 proportion. This is explained on the hypothesis that two pairs of factors are involved in the interaction as indicated below : -

Parents : Grey grained type **$Pr_1\ Pr_1\ pr_2\ pr_2$** · Grey grained type **$pr_1\ pr_1\ Pr_2\ Pr_2$**

↓

F_1 : Red grained

$Pr_1\ pr_1\ Pr_2\ pr_2$

Gametes from F_1 **$Pr_1\ Pr_2$, $Pr_1\ pr_2$, $pr_1\ Pr_2$, $pr_1\ pr_2$**

The F_2 gametic combinations are shown in the checker board, (Fig. 17).

It will be seen from the checker board that the two factors, Pr_1 and Pr_2, have individually the same effect, viz., they produce grey coloured grains. Whenever these dominant factors are brought together, they interact and produce red grains. In the checker board (Fig. 17) it will be seen that in 9/16 cases the dominant factors interact and produce red grains. The double recessive also is grey grained. Therefore, the last three classes of phenotypes in the normal 9 : 3 : 3 : 1 ratio are indistinguishable from one another, with the result that the dihybrid ratio is modified to 9 : 7 ratio,

The F_2 data may be summarised as shown below :-

TABLE 8.

Phenotype.	Fre-quency.	Genotype.	Fre-quency.	F_3 behaviour.
Red ...	9	$Pr_1\ Pr_1\ Pr_2\ Pr_2$	1	Breeds pure.
		$Pr_1\ Pr_1\ Pr_2\ pr_2$	2	Segregates into 3 brown : 1 white.
		$Pr_1\ pr_1\ Pr_2\ Pr_2$	2	Do.
		$Pr_1\ pr_1\ Pr_2\ pr_2$	4	Segregates like F_1.
Grey ...	7	$Pr_1\ Pr_1\ pr_2\ pr_2$	1	Breeds pure.
		$Pr_1\ pr_1\ pr_2\ pr_2$	2	Segregates for factor Pr_1—pr_1 but is all phenotypically white.
		$pr_1\ pr_1\ Pr_2\ Pr_2$	1	Breeds pure.
		$pr_1\ pr_1\ Pr_2\ pr_2$	2	Segregates for factor Pr_2—pr_2 but is phenotypically all white.
		$pr_1\ pr_1\ pr_2\ pr_2$	1	Breeds pure.

The seven grey types fall into five genotypes. Their genotypic differences can be distinguished by crossing tests. For example, the grey with genotype $pr_1\ pr_1\ pr_2\ pr_2$ when crossed with the grey parent of the genotype $Pr_1\ Pr_1\ pr_2\ pr_2$ or $pr_1\ pr_1\ Pr_2\ Pr_2$ results in grey grained F_1. In contrast to this, the grey with genotype $pr_1\ pr_1\ Pr_2\ pr_2$ when crossed with $Pr_1\ Pr_1\ pr_2\ pr_2$ results in 3 Red to 1 grey in the first generation of the cross ; the same grey when crossed with $pr_1\ pr_1\ Pr_2\ Pr_2$ results in grey grained types only. The five genotypes can be distinguished by such crossing tests.

The complementary ratio results by the modification of 9 : 3 : 3 : 1 ratio, where the three latter classes of phenotypes merge into one and are externally indistinguishable. The two parents, which are similar in respect of a character give rise to a new character when they are crossed and in F_2 segregation 9 new types and 7 parental types appear. This type of interaction is termed complementary.

The type of interaction between the two factors Pr_1 and Pr_2 is comparable to that between two colourless chemicals which when mixed produce colour. For example, phenolphthalein when added to KOH produces pink colour though both the reagents are colourless. However this does not mean that complementary ratios can be expected in cases of colour production only.

4. **Supplementary Factors (9 : 3 : 4 ratio).**—In the genetic analysis of glume colour in cholam it was found that two factors P and Q interact. Under Section 4 of the preceding chapter it was pointed out that blackish-purple is governed by the factor-pair P-p. When Q is present along with P, the glume

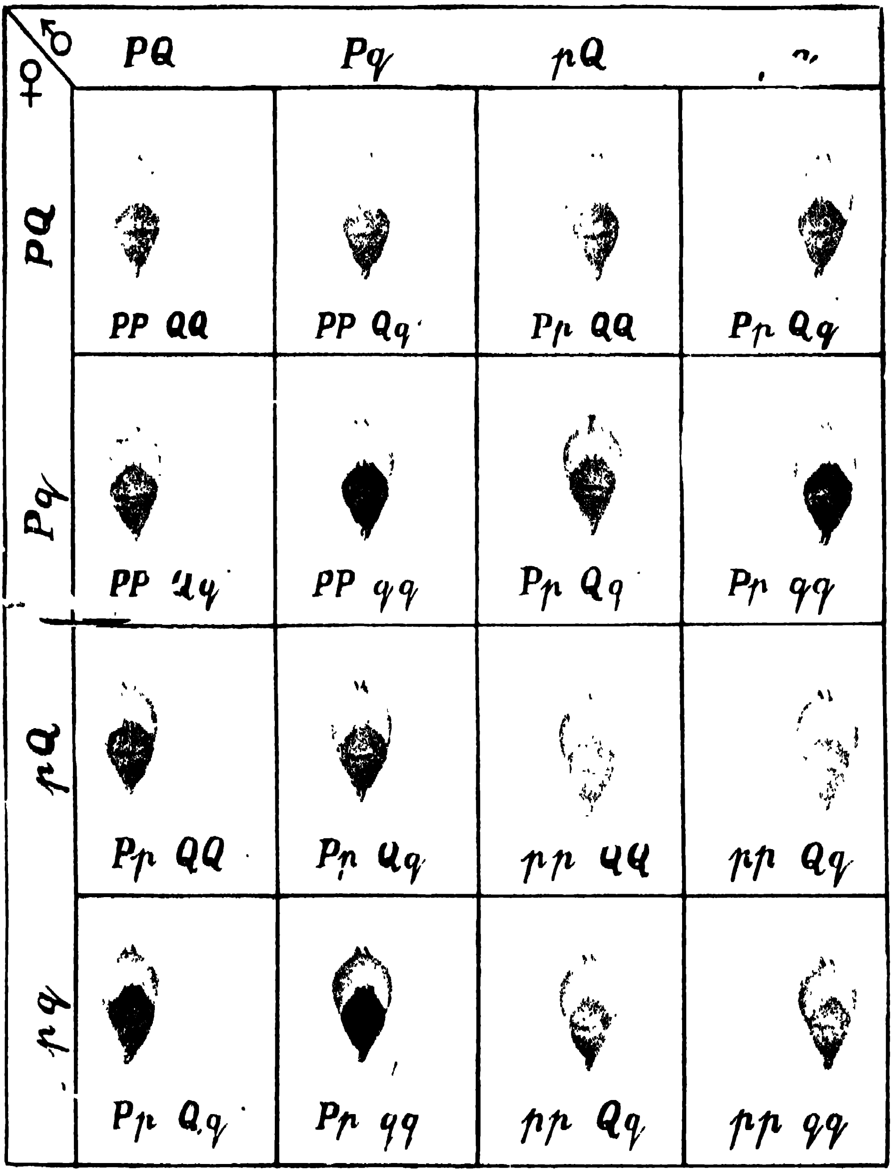

Fig. 18.—Supplementary Factors (9 : 3 : 4 Ratio).

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colour is modified to reddish purple. The factor Q has no effect by itself in the absence of the dominant factor P. The factorial scheme of such a cross between blackish purple and brown glumed variety is shown below :—

Parents :	Blackish purple **PPqq**	×	Brown **ppQQ**
F_1		Reddish purple **Pp Qq**	
Gametes of F_1 :	**PQ , Pq , pQ , pq .**		

The F_2 gametic combinations are shown in the following checker board (Fig. 18).

The brown glumed parent has the dominant factor Q and this factor is without any effect on glume colour in the absence of P. Therefore the two genotypes ppqq and ppQQ are both phenotypically brown glumed.

The F_2 data may be summarised as shown below :—

TABLE 9.

Phenotype.	Frequency.	Genotype.	Frequency.	F_3 behaviour.
Reddish purple ...	9	PPQQ	1	Breeds pure.
		PPQq	2	Segregates into 3 reddish purple : 1 blackish purple.
		PpQQ	2	Segregates into 3 reddish purple : 1 brown.
		PpQq	4	Segregates like F_1.
Blackish purple ...	3	PPqq	1	Breeds pure.
		Ppqq	2	Segregates into 3 blackish purple : 1 brown.
Brown ..	4	ppQQ	1	Breeds pure.
		ppQq	2	Segregates for factor Q-q but is phenotypically brown.
		ppqq	1	Breeds pure.

Of the pure breeding brown glumed types, ppQQ carries the interacting factor Q while ppqq does not. When crossed with the blackish purple the former results in reddish purple glumed F_1 and the latter in blackish purple glumed one.

The modification of 9 : 3 : 3 : 1 into 9 : 3 : 4 arises due to the fact that the last two genotypes of the former are phenotypically alike and are indistinguishable. The two pairs of factors involved in this modification affect the same character, one of the factors having visible effect by itself while the other has none by itself but when the two factors are brought together they interact and produce new effect.

5. **Epistasis (12 : 3 : 1 ratio).**—This modification of F_2 ratio may be explained by taking an example from cholam. The grains in this crop may be pearly or chalky in appearance. Many of the cultivated types show pearly grains which are shining and translucent. They are lustrous and oily white. In contrast to this, chalky grains bear no lustre and are opaque and salt white. These are characterised by a large deposit of starch in mesocarp layer. The deposit is uneven giving banded appearance to the grain. Pearly is monogenic dominant over 'chalky' (Z-z). In regard to colour of grain it may be red or white. Red is monogenic dominant over white (W-w). When a red grained type is crossed with white pearly, F_1 is red grained but whether it is pearly or chalky cannot be distinguished due to the presence of colour in seed coat. The character, colour of grain, masks the character of appearance of grain. The factorial representation of this cross is shown below :—

Parents : Red WWzz × White pearly wwZZ

F_1 Red WwZz

Gametes of F_1 : WZ, Wz, wZ, wz.

Gametic combinations of F_2 are shown in the checker board (Fig. 19).

The character, chalkiness or pearliness of grain is masked by the colour of grain. The F_2 data may be summarised as follows :—

TABLE 10.

Phenotype.	Frequency.	Genotype.	Frequency.	F_3 behaviour.
Red	12	WWZZ	1	Breeds pure.
		WwZZ	2	Segregates into 3 red : 1 white pearly.
		WWZz	2	Segregates for the factor pair Z-z but is all phenotypically red.
		WwZz	4	Segregates like F_1.
		WWzz	1	Breeds pure.
		Wwzz	2	Segregates into 3 red : 1 white chalky.
White pearly ...	3	wwZZ	1	Breeds pure.
		wwZz	2	Segregates into 3 white pearly : 1 white chalky.
White chalky ...	1	wwzz	1	Breeds pure.

The 12 red types really fall into two classes *viz.*, 9 red pearly and 3 red chalky, but this grouping is rendered difficult and the colour masks the difference between pearly and chalky. The two dominant factors affect the same character or organ with the result that one of them expresses itself while the expression of the other is masked. The phenomenon of masking is termed *epistasis*. The masking factor is epistatic to the masked factor and conversely the masked factor is hypostatic to the masking factor. In the above example W is epistatic to Z and conversely Z is hypostatic to W.

CHECKER BOARD

	WZ	Wz	wZ	wz
WZ	WWZZ RED	WWZz RED	WwZZ RED	WwZz RED
Wz	WWZz RED	WWzz RED	WwZz RED	Wwzz RED
wZ	WwZZ RED	WwZz RED	wwZZ WHITE PEARLY	wwZz WHITE PEARLY
wz	WwZz RED	Wwzz RED	wwZz WHITE PEARLY	wwzz WHITE CHALKY

Fig. 19. *Epistasis* (12 : 3 : 1 ratio) *Note* that when the grain is red, pearly or chalky appearance is masked.

The phenomenon of epistasis is different from dominance. Dominance relates to allelomorphic pair of factors. The two pairs of factors involved in epistasis are not allelomorphic and they may be situated on different chromosomes.

6. **Inhibitory Factor 13 : 3 ratio.**—Two pairs of factors are involved here and one of the dominants suppresses or inhibits the expression of the other dominant. This may be explained by taking pigmentation in rice plants. In a cross between a purple pigmented and a green rice plant it was found

that the F_1 was green and in F_2 there appeared 13 green and 3 purple pigmented types. This is explained on the following hypothesis :

Parents :	Green **II lp lp**	×	Purple **ii Lp Lp**
F_1		Green **Ii Lp lp**	
Gametes of F_1		**ILp, Ilp, iLp, ilp.**	

The F_2 gametic combinations and phenotypes are shown in the checker board (Fig. 20).

The factor Lp is capable of producing purple colour in leaves and is present in one of the parents. The parent with green leaves possesses a factor. 'I' which has no visible effect by itself but it inhibits the colour production by 'Lp.' The presence of the inhibiting factor can be judged only by its action on the factor Lp and not by any phenotypic effect of its own. The F_2 results of the cross are summarised below :—

TABLE 11.

Phenotype.	Frequency.	Genotype.	Frequency.	F_3 behaviour.
Green ...	13	II LpLp	1	Breeds pure.
		II Lplp	2	Segregates for factor Lp but phenotypically breeds pure for green.
		II lplp	1	Breeds pure.
		Ii Lplp	4	Segregates like F_1.
		Ii lplp	2	Segregates for factor I, but phenotypically breeds pure for green.
		Ii LpLp	2	Segregates into 3 green : 1 purple.
		ii lplp	1	Breeds pure.
Purple ...	3	ii LpLp	1	Breeds pure.
		ii Lplp	2	Segregates into 3 purple : 1 green.

Genotypes II LpLp, II Lplp, II lplp, Ii lplp and iilplp though phenotypically breed pure for green, possess different potentialities to produce purple colour when crossed with suitable genotypes. In this type of modification, the visible, effects of the segregation of the factor Lp-lp is obliterated by the inhibiting effects of factor I.

The first instance of inhibiting factor was met with in the case of plume colour in fowls. White Wyandotte and White Leghorn are two breeds of fowls with white plumes. The white plumes in Wyandottes proved simple monogenic recessive to coloured plumes. When the leghorn was crossed with fowls with coloured plumes, the F_1 was white and in F_2, 13 white : 3 coloured types appeared. Therefore, two pairs of factors are involved here. The factor for inhibiting colour in plumes is present in white Leghorn. If the inhibiting

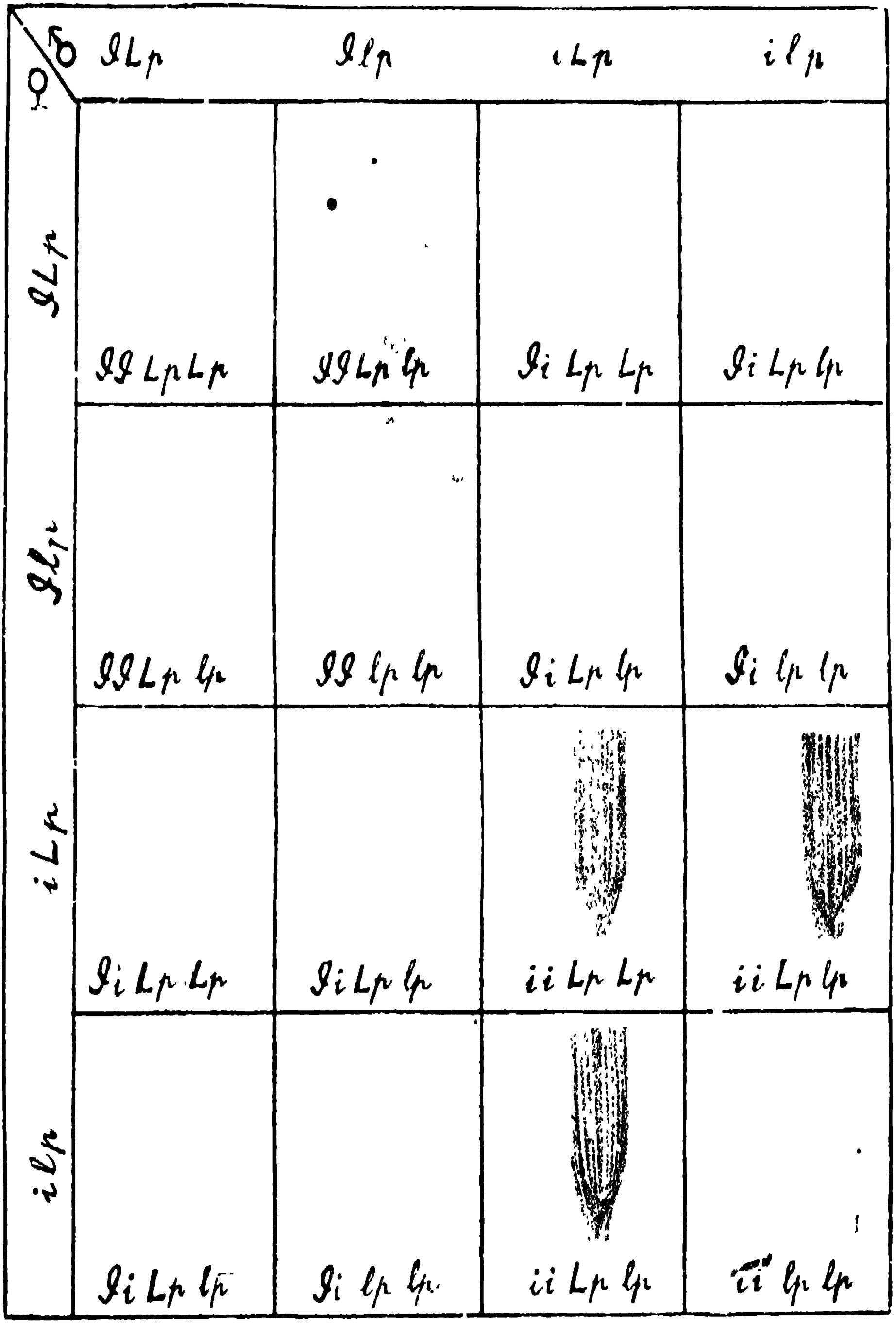

Fig. 20. INHIBITORY FACTOR. When I is present, colour is inhibited. By itself I does not show any phenotypic effect in the absence of Lp. Note the possible genotypes for green — I Lp, I lp, i lp.

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factor is symbolised as I-i and the colour factor C-c, the genotype of the two white breeds of fowls may be symbolised as shown below :—

White Wyandotte	iicc
White Leghorn	IICC

Such inhibiting factors have been frequently met with in plants.

7. **Duplicate Factors (15 : 1 ratio).**—As an example for this type of modification, the character pair 'awned-awnless' in rice may be taken. In a cross between 'awned' and 'awnless' types, F_1 was awned and in F_2, 15 awned and 1 awnless types appeared. This shows that two pairs of factors are involved in the cross. If the factors are designated A_1, A_2, the following factorial constitution will represent a cross between awned and awnless types.

Parents	Awned	×	Awnless
	$A_1A_1A_2A_2$	↓	$a_1a_1a_2a_2$
F_1		Awned	
		$A_1a_1A_2a_2$	
Gametes of F_1		A_1A_2, A_1a_2, a_1A_2, a_1a_2	

The F_2 genotypes and phenotypes are shown in the following checker board (Fig. 21).

CHECKER BOARD

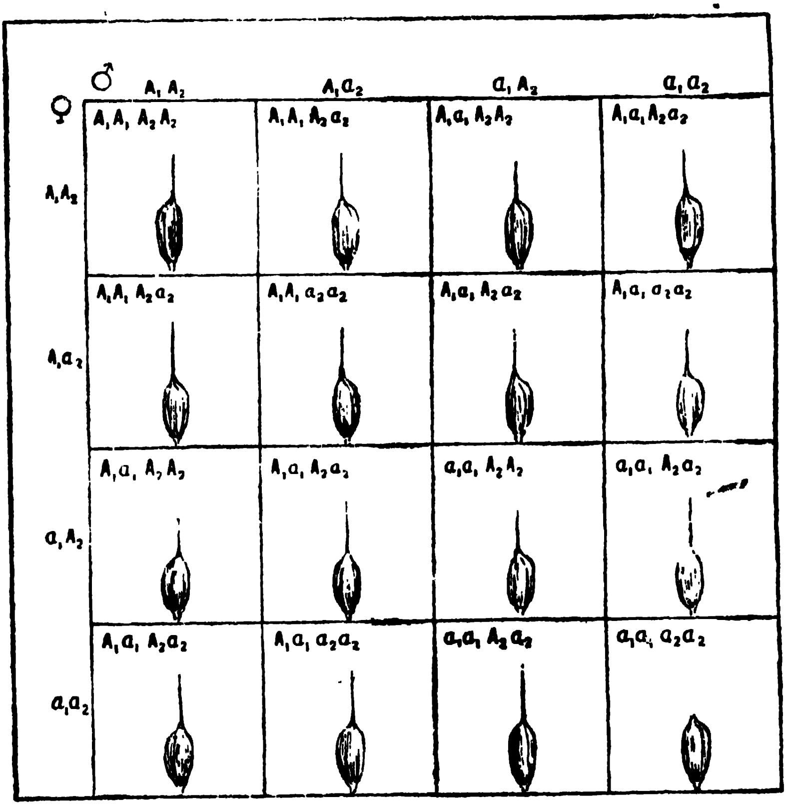

Fig. 21.—Duplicate Factors (15 : 1). Note that the presence of any one factor A_1 or A_2 causes awn. Absence of both the factors causes awnless grain.

15 : 1 ratio arises when two factors affecting the same character produce similar effects when both are present or only one is present. Absence of both the factors causes the development of the recessive character ' awnless '.

That two pairs of factors can act indentically is a point of importance to a plant breeder. This condition arises by the duplication of genes which originally existed singly. This is generally the case with polyploids. The first three classes of phenotypes in the normal 9 : 3 : 3 : 1 ratio merge into one class.

The F_2 data may be summarised as shown below :—

TABLE 12.

Phenotype.	Frequency.	Genotype.	Frequency.	F_3 behaviour.
Awned ..	15	$A_1 A_1 A_2 A_2$	1	Breeds pure.
		$A_1 A_1 A_2 a_2$	2	Segregates for factors A_2-a_2 but phenotypically breeds pure for awned.
		$A_1 a_1 A_2 A_2$	2	Segregates for factors A_1-a_1 but phenotypically breeds pure for awned.
		$A_1 a_1 A_2 a_2$	4	Segregates like F_1.
		$A_1 A_1 a_2 a_2$	1	Breeds pure.
		$a_1 a_1 A_2 A_2$	1	Do.
		$a_1 a_1 A_2 a_2$	2	Segregates into 3 awned : 1 awnless.
		$A_1 a_1 a_2 a_2$	1	Do.
Awnless		$a_1 a_1 a_2 a_2$	1	Breeds pure.

The double recessive ' awnless ' appears in 1/16 of the F_2 population. In the case of duplicate factors there are two phenotypes only and the recessive one appears in one-sixteenth of the F_2 population, a proportion which is less than in any other modification of dihybrid. The reduction of the recessive character to this low level is advantageous in cases where the recessive character is not economically desirable. For example, albinism in ragi is governed by duplicate factors and from heterozygous plants albinos are thrown out in the ratio 15 green to 1 albino. Albinism is an undesirable character and the danger of its appearance even from natural crosses is reduced to low level by the duplicate factors.

8. **Polymerism (9 : 6 : 1 ratio).**—The pericarp colour in wheat may be deep red, light red or colourless. When two types with deep red and colourless pericarp are crossed, F_1 is deep red. In F_2, 9 deep red, 6 light red and 1

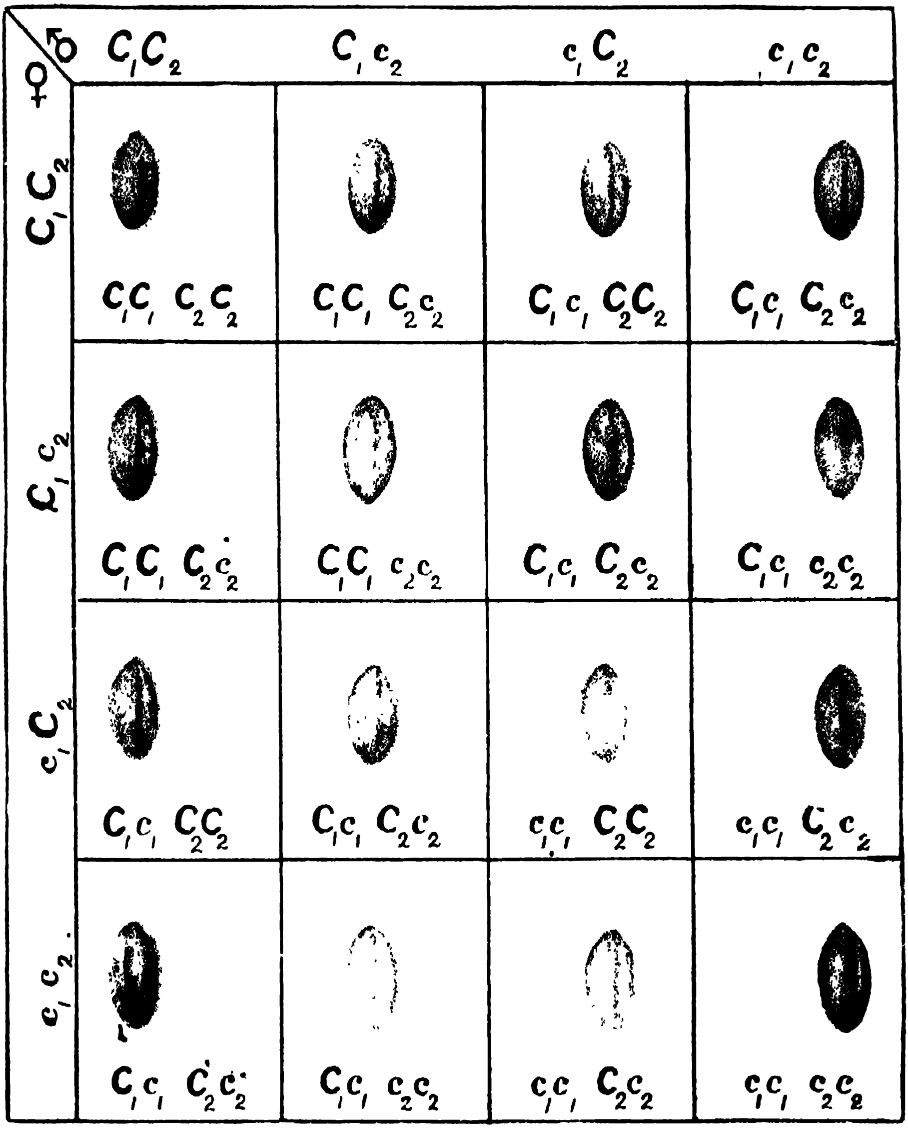

Fig. 22. POLYMERISM. 9 : 6 : 1 Ratio. When both C_1 and C_2 are present the colour is deep red. When any one factor is present the colour is light Red. When both are absent the grain is colourless. The two factors C_1 and C_2 show cumulative effect

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colourless types appear. This genetic behaviour may be explained on the hypothesis that there are two pairs of factors C_1 and C_2 involved in the cross.

Parents: Deep red $C_1C_1C_2C_2$ × White $c_1c_1c_2c_2$

F_1 : Deep red $C_1\ c_1\ C_2\ c_2$

Gametes of F_1 : C_1C_2, C_1c_2, c_1C_2, c_1c_2.

The F_2 Gametic Combinations are shown in Fig 22, and the F_2 data are summarised below in table 13.

TABLE 13.

Phenotype.	Frequency.	Genotype.	Frequency.	F_3 behaviour
Deep red ...	9	$C_1\ C_1\ C_2\ C_2$	1	Breeds pure.
		$C_1\ C_1\ C_2\ c_2$	2	Segregates into 3 deep red : 1 light red.
		$C_1\ c_1\ C_2\ C_2$	2	Do.
		$C_1\ c_1\ C_2\ c_2$	4	Segregates like F_1.
Light red ...	6	$C_1\ C_1\ c_2\ c_2$	1	Breeds pure.
		$C_1\ c_1\ c_2\ c_2$	2	Segregates into 3 light red : 1 colourless.
		$c_1\ c_1\ C_2\ C_2$	1	Breeds pure.
		$c_1\ c_1\ C_2\ c_2$	2	Segregates into 3 light red : 1 colourless.
Colourless ...	1	$c_1\ c_1\ c_2\ c_2$	1	Breeds pure.

In this type of modification two dominant factors affecting the same trait have similar effect when present individually but when both are present they produce double the effect. The middle two classes of phenotypes in 9 : 3 : 3 : 1 become indistinguishable. They show *additive effect.* This is the simplest case where the factors show additive effect. If the principle is extended to a large number of factors, a graded effect can be seen in the phenotype. With gradual increase in the number of dominant factors, the character expression also proportionately increases. Such characters are termed *quantitative characters.*

9. **Modifications due to incomplete dominance (3 : 6 : 3 : 1 : 2 : 1).**— In cases of monogenic difference, 3 : 1 ratio is modified into 1 : 2 : 1. In the case of a dihybrid, if dominance is incomplete in one of the pairs of characters, 9 : 3 : 3 : 1 is modified to (3 : 1) (1 : 2 : 1) or 3 : 6 : 3 : 1 : 2 : 1.

An instance of this type was noted in rice in regard to the character pairs 'dense-lax' panicles and 'clustered-nonclustered' spikelets. (Fig. 23).

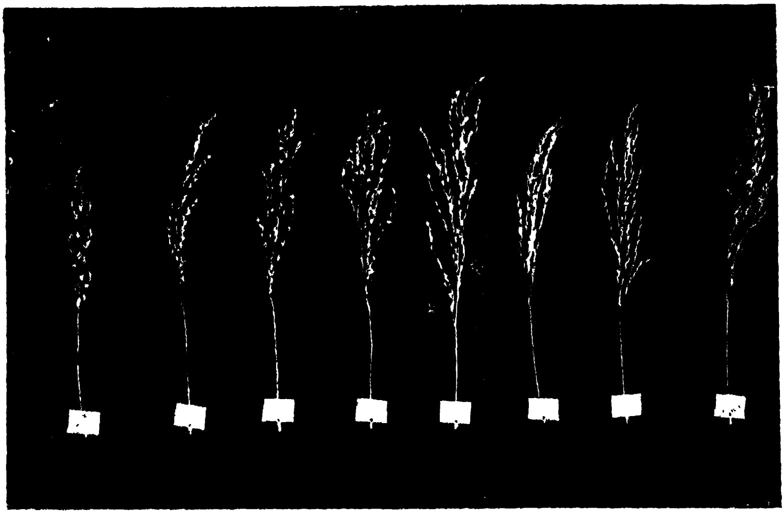

Fig. 23.—The central six types show F_2 recombinations in a cross.

T298 is a type with dense panicle and nonclustered spikelets and E. B. 331 is another type with lax panicle and clustered spikelets. Lax panicle is dominant to dense panicle and clustered spikelet is partially dominant over non-clustered spikelets. In F_2 segregation 6 classes of phenotypes appear as shown in Figures 23 and 24.

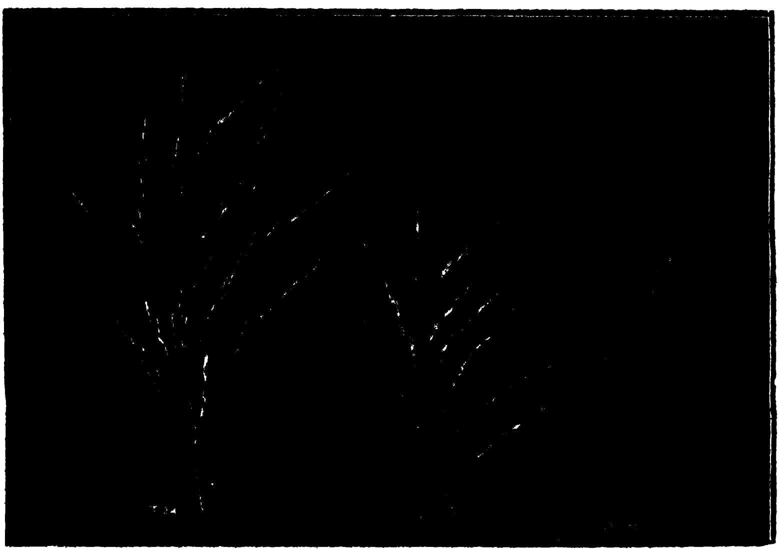

Fig. 24.—Parents and F_1 to show clustering of grain and panicle shape.

TABLE 14.

F_2 segregation in the cross T. 298 × EB. 331.

	Typical cluster lax panicle.	Inter-mediate cluster lax panicle.	No cluster lax panicle.	Cluster and dense panicle.	Inter-mediate cluster and dense panicle.	No cluster but dense panicle.
	SS CC or Ss CC	SS Cc or Ss Cc	SS cc or Ss cc	ss CC	ss Cc	ss cc
Observed ...	1173	2435	1183	298	706	520
Expected on 3 : 6 : 3 : 1 : 2 : 1 ratio.	1185	2370	1185	395	790	395

10. **Lethal Factor.**—All genetic factors are not useful to the plant. There are some factors which develop harmful characters which may cause death to the progeny. Even if the plant possesses scores of other desirable factors, one harmful factor may cause life impossible. For example, in the case of plants, presence of chlorophyll is essential for normal development and in its absence the plant dies by starvation. This important character is very often governed by a single factor.

In the case of pearl millet it was found that factor ' C ' is responsible for chlorophyll and count in segregating families showed 10,101 green to 3,390 albino seedlings which is an approximation to 3 : 1 ratio. The albino seedlings die a few days after germination.

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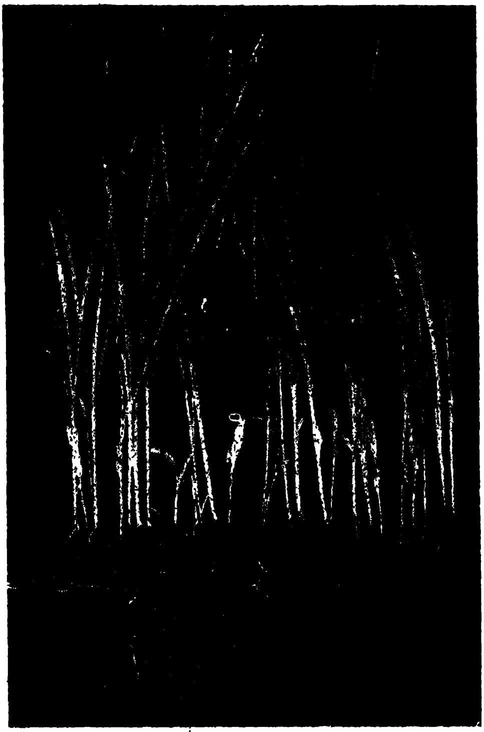
Fig. 25.—Albino seedlings in rice. The white seedlings lack chlorophyll and hence they die out.

Various types of chlorophyll deficiencies have been recorded in different crops like maize, rice, cholam, etc. The deficient types may die a few days

after germination or they may recover from the deficiency and become normally green. For example, in rice it was found that (1) lethal yellow (yy) seedlings die after about 8--10 days' growth in the nursery (2) lutescent seedlings (*ll*) which are normal green to start with turn yellow and die off (3) yellow and white striped seedlings are weak and slow growing at first but they turn green a fortnight after germination (4) green and yellow striped seedlings (ggyy) turn green 8—10 days after germination (5) albinos (ww) die a few days after germination. (Fig. 25).

Even though the seedlings may be green and normal, the lethal effect may be caused by a lethal factor. In *Sorghum caudatum* it was noticed that one month old seedlings were dying due to atrophy of roots and shoots. Lethal green seedlings were recessive to normal green (CL-cl) (Fig. 26).



(*With the kind permission of Curr. Sc.*)

Fig. 26.—Lethal green seedlings of cholam. Note the small seedlings which die out. The lethal effect is caused by the recessive genetic factor *cl*.

The Lethal effect may be brought about at any stage during the development of the zygote. The zygote itself may perish or the death may take place before the embryo is fully formed. When death takes place before the embryo is formed the F_2 ratios are altered due to the non-appearance of the lethal class. For example, in mice yellow coat colour is a heterozygous character (Yy) and it always segregates and never breeds true. When two yellows are mated, in the progenies, for every two yellow types one coloured

type appears. When the yellows are mated to non-yellows half the progenies are yellow and the other half are non-yellow. This latter cross is equivalent to back-cross of the heterozygous type with the recessive parent. Therefore the results of the matings between the two yellows may be represented as shown below :—

Yellow Yy	×	yellow Yy	
	↓		
YY	yellow Yy	yellow Yy	Black yy

The homozygous dominant YY is lethal and the F_2 ratio is modified to 2 : 1 (Fig. 27).

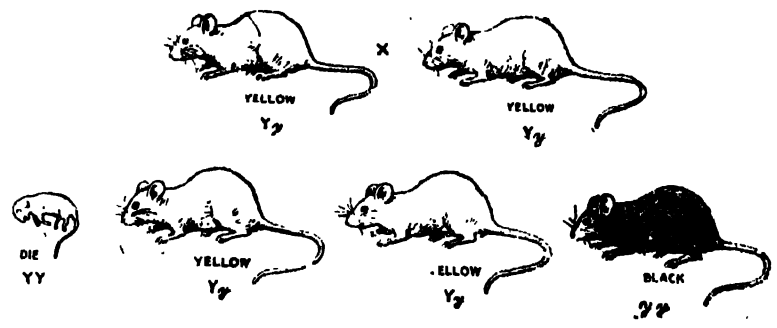


Fig. 27.—Lethal factor in rats. Note that the homozygous YY die out.

A consideration of lethal factors is important in plant breeding. The lethal factors cause death when they are in homozygous condition. The death may occur at any stage of development of the plant. In plant breeding it is the experience that naturally cross-fertilised plants when artificially self fertilised throw out abnormal types. The abnormal types arise due to the fact that selfing renders many genetic factors homozygous and the latter bring about deleterious effects of different grades.

11. **Mosaic Expression.**—In some instances it is found that the F_1 phenotype is a resultant of mosaic expression of both dominent and recessive phenotypes. The Andalusian fowls are blue in colour and this is a heterozygous character. In the breed when black feathered type is crossed with white-splashed-with-blue type, the hybrid is blue feathered. The two parental types are pure breeding when crossed *inter se*. The black feathered type is due to homozygous factor developing that character. In these feathers the pigment is black in colour and the rod shaped black granules are evenly distributed in the cells of the feather. In the blue feathers of the other parent, the pigment bodies are blue round and clumped and the barbules of feathers are not pigmented. When the pigmentation of the hybrid is studied, it is found that all feathers are pigmented as in the black parent but in the distribution of pigment it resembles the other parent. Thus the mosaic expression of the two parental characters in the matter of details of pigmentation causes the blue

hybrid. Andalusian blue never breeds true when mated *inter se* and it gives rise to 1 black : 2 blue : 1 white splashed with blue and hence the character cannot be fixed as pure breeding. It is always heterozygous.

As another example for mosaic expression of the parental characters in the hybrid may be mentioned the cross between red and white type of short horn breed in cattle. The hybrid is roan in colour which is an intermediate type between the parental characters. The roan colour is caused by a fine mixture of hairs of red and white in a mosaic fashion.

12. **Variable dominance.**—Even though the inheritance of a character is governed by a single pair of allelomorphs in a cross the separation of phenotypes into distinct parental groups may be difficult. Thus in the case of seed coat colour in red-gram, type 5 was silver white with faint grey markings and type 80 was fawn with brown markings. In F_2, separation of phenotypes was difficult due to variability between the parental forms. In the case of *Drosophila*, when ebony and sooty coloured types are crossed, the F_1 colour is variable from ebony to sooty. Again the F_2 classification is difficult without further breeding tests.

13. **Cytoplasmic effect.**—The cytoplasmic effect is wide and the general principles will be discussed later. In an earlier section it was pointed out that genotypically the reciprocal crosses are identical. However, in many cases the reciprocal crosses show phenotypical differences and these are due to cytoplasmic differences. The female gamete in higher plants is surrounded by a large section of sterile tissues and the ovum grows to maturity, both before and after fertilisation, attached to the female parent. The cytoplasm surrounding the male gamete *viz.*, the pollen is comparatively negligible.

Reciprocal cross differences have been reported in a large number of instances. For example, 38 races of *Epilobium hirsutum* were crossed reciprocally with the race *jena*. All hybrids with *jena* as male parent showed normal vigour but in the reciprocal cross a continuous series of abnormalities were observed in F_1, depending upon the race of male parent. It was evident that the *jena* plasma reacted with inhibiting effects on the genotypes of the different male parents. In the course of hybridisation work in cambodia cotton, reciprocal cross differences have been met with at Coimbatore.

14. **Endosperm character.**—In maize there are two types of endosperm : floury and flinty. In reciprocal crosses between the two, the F_1 endosperm was after the mother. Endosperm develops from secondary nucleus resulting from the fusion of two maternal and one paternal nuclei each one containing haploid set of chromosomes. Therefore, endosperm in all cases is triploid. (3n). If F represents, flinty endosperm and f floury, F is dominant over f in diploid heterozygous tissues (Ff). The genotype of the endosperm of pure flinty type is *FFF* and that of floury type is *fff*. In a cross between flinty and floury, the hybrid endosperm is *FFf* and in the reciprocal cross it is *ffF*. When ' floury ' type is crossed to flinty, the hybrid endosperm is floury because there are two recessive factors and one dominant factor in the genotype *ffF*. In this instance, two doses of recessive factors express themselves phenoty-

pically against a single dose of a dominant factor. This is termed *dosage effect.*

The dosage effect is not evidenced in all cases of the endosperm characters. For example, sugary x starchy gives starchy hybrid and the reciprocal hybrid also shows starchy endosperm. In this character dominance is not altered by dosage of the concerned genes.

15. **Xenia.**—Normally when two parents are crossed, the seeds that develop from crossed flowers represent the F_1 generation. When sown they germinate and give rise to the hybrid plant which on maturing bears seeds representing the second generation of the cross. The crossed seed in general is not different from the other seeds borne on the same mother plant ; similarly, seeds of F_1 plant are all alike, but when sown exhibit genetic difference in the seedling or seed characters. But in the case of some plants, in reference to endospermous seeds and in respect of certain seed characters, the genetic differences are realised one year sooner. The seed itself exhibits genetic differences in the embryo within. Thus, in the maize plant the crossed seeds developing on the parent plant after crossing may exhibit change in form or colour, when dominant factors are introduced through the pollen parent, *e.g.*, when sweet corn with wrinkled translucent kernels is pollinated by field corn with smooth opaque seeds, the seeds of crossed ears are smooth opaque. The F_1 plants when selfed show ears with 3 smooth opaque : 1 wrinkled translucent seeds. The segregation is evidenced one year earlier than in other cases. This phenomenon is termed *Xenia.*

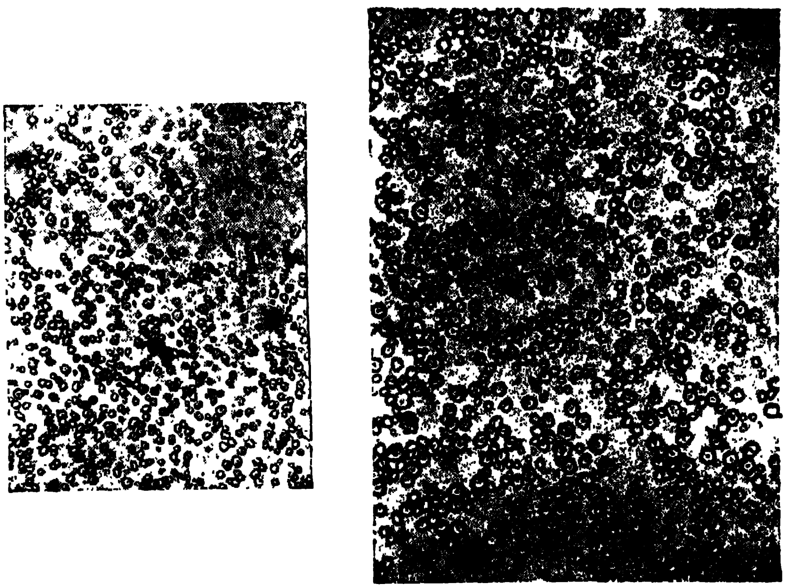


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Fig. 28.—The starch granules of dimpled (left) and non-dimpled (right) cholam grains.

A case of Xenia has been noted in cholam. The variety " Sakkara gulige jonna " of Bellary district (Madras) shows dimpled grains. These plants

are not vigorous. Non-dimpled grains are dominant over dimpled giving 3 : 1 ratio in F_2. When A. S. 219 (dimpled grain) was crossed with A. S. 158 (non-dimpled grain), the ears of F_1 plant showed both dimpled and non-dimpled grains and the counts from 49 plants are presented in table 15. The starch granules in these two types, of grains differ as shown in figure 28.

TABLE 15.

COUNTS OF NON-DIMPLED AND DIMPLED GRAINS IN HYBRID EAR-HEADS

Serial No.	Non-dimpled.	Dimpled.	% Dimpled.	Serial No.	Non-dimpled.	Dimpled.	% Dimpled.
1	2,159	716	24·9	26	2,833	732	20·2
2	911	2844	24·0	27	1,617	415	20·4
3	1,268	401	24·0	28	1,910	487	20·3
4	3,037	916	23·2	29	2,193	553	20·1
5	1,087	318	23·0	30	1,464	378	20·0
6	1,706	510	23·0	31	1,971	489	19·9
7	1,934	569	22·7	32	2,340	573	19·7
8	2,110	613	22·5	33	2,081	509	19·7
9	2,029	582	22·3	34	1,497	366	19·7
10	2,683	770	22·3	35	1,804	366	19·6
11	2,019	578	22·2	36	2,240	542	19·5
12	1,468	416	22·1	37	2,190	532	19·5
13	1,423	460	22·1	38	2,353	572	19·5
14	1,995	337	22·0	39	1,332	322	19·5
15	1,648	424	22·0	40	2,440	589	19·4
16	2,085	590	22·0	41	1,466	351	19·3
17	2,933	322	21·9	42	1,638	385	19·0
18	2,285	636	21·8	43	1,944	487	19·0
19	1,716	471	21·5	44	2,093	488	18·9
20	2,211	597	21·3	45	2,931	682	18·9
21	2,736	733	21·1	46	2,629	606	18·7
22	2,397	635	20·9	47	2,609	597	18·6
23	1,738	488	20·9	48	2,956	675	18·6
24	2,392	628	20·8	49	1,579	425	21·0
25	2,530	685	20·6				
					99,710	26,250	20·8

In rice, glutinous flowers when pollinated by pollen from starchy type, develop starchy grains. F_1 plants when selfed, bear a mixture of starchy and glutinous grains (Fig. 29). For 9 F_1 plants, counts of grains in ears are shown below :—

		Starchy	glutinous.
Total for 9 F_1 plants	...	5292	1587
Expected on 3 : 1 ratio	...	5159	1720

There is slight excess of starchy types and this has been later explained as probably due to the glutinous pollen being weaker in its action.

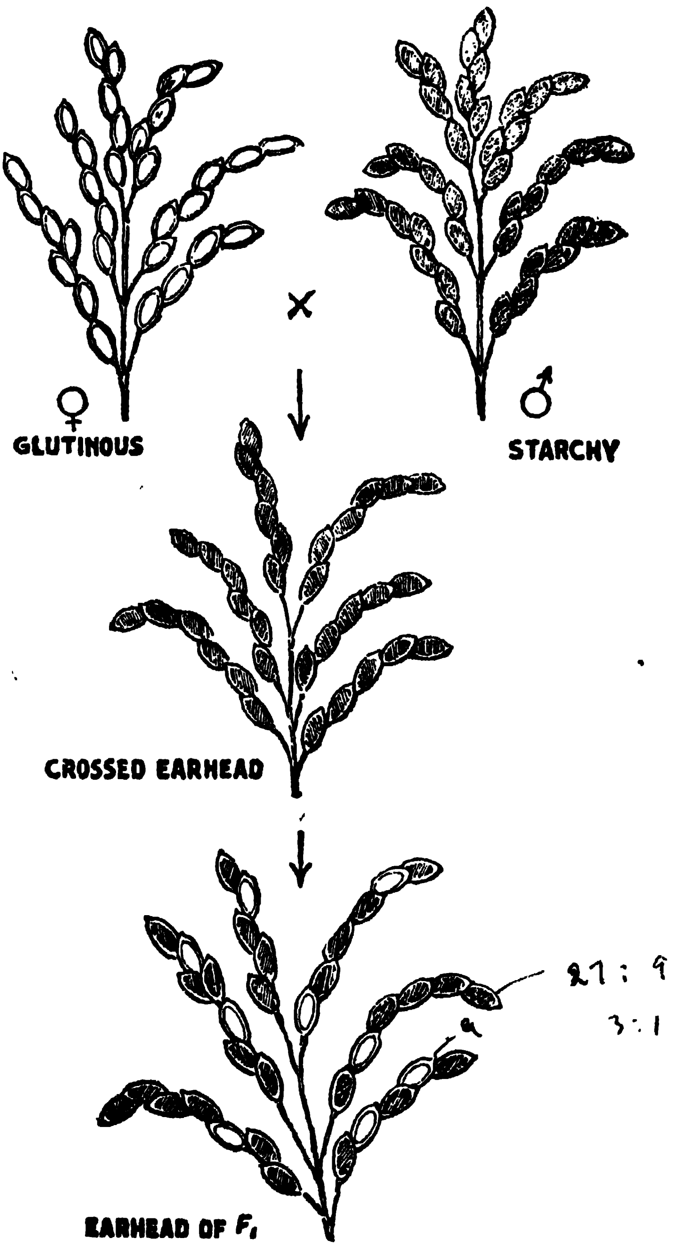


Fig. 29.—Diagram to explain xenia in the cross glutinous X starchy rice. Note that the crossed seeds are starchy and the segregation in 3 : 1 ratio is evident even in the earhead of the F_1 plant.

The term Xenia was first used by Focke in 1881. This was applied to the effect of foreign pollen on the form or colour in any part of the plant. This may fall into three groups (1) where the zygote is affected (2) where the endosperm characters are affected (3) where the effect is on maternal tissues. In the first two groups, the genotype of the pollen has direct influence but in

the third group it has none. The effect of foreign pollen on maternal tissues was suggested to be due to secretion of hormones by endosperm and embryo (Swingle 1928) and the secretions have specific influence on maternal tissues depending upon the pollen parent. In dates, the time of maturity can be made to vary according to the pollen parent. In certain varieties of cotton, length of lint differs in different pollinations (Harrison 1931). Differences in time of maturity, size, form, colour, etc., of fruits of various plants are also reported. In some instances, number and condition of developing seed within the fruits are also directly affected by different pollinations.

The term *metaxenia* was introduced by Swingle (1926) to denote " influence of male parent on the tissues of the mother plant outside the embryo and endosperm especially as exemplified in the date palm." In oranges, shape, colour and flavour of fruits have been reported to be affected by pollen. In apple the variety golden spire, on self-pollination, develops parthenocarpic fruit which are different in form from cross-pollinated true fruits. Differences in acidity are also reported due to pollen parents.

16. **Heterosis.**—In respect of certain characters such as height, size, weight and vigour, the hybrid exceeds the dominant parent. This is termed *hybrid vigour* or *heterosis*. Ashby attributes this hybrid vigour to the initial advantage gained by the hybrid embryo by being bigger than the parental embryos. East 1936 has shown that heterosis is a gene controlled process. Heterosis is greater when the disparity between the parents is large. In type and extent heterosis differs in different genera. In practical breeding problems heterosis is an important phenomenon. It concerns the whole plant. In the case of cross fertilised plants like maize, self-fertilisation leads to reduction in vigour and unmasking of deleterious recessive genes. When the plants are rendered homozygous, they are inferior to the commercial parental types. When these homozygous types are crossed, heterosis is great and the hybrids in some cases excel the parents and the commercial forms. (*Vide* Chapter XIX also).

17. **Gene symbols.**—Extensive work has been done in genetic analysis of crop plants such as maize, rice, cholam, cotton, etc. It is necessary that gene symbols should be standardised to avoid confusion. When standard symbols are used, it is easy to identify the genes distributed in different varieties or geographical races. When such lists are completed in respect of a crop, the plant breeder can know the source of availability of any one gene and also about its mode of inheritance, etc. Attempts have been made in this direction and gene symbols for some crops have been published in various research publications. The following are some of the main principles underlying gene symbolisation :

(1) Genetic analysis on an extensive scale is necessary to understand the inter-relationship of genes within the species as well as to bring out the similarity of genes affecting the same type of character in different species. The symbolisation in maize may be taken as working model as it is the only crop plant where the genetic analysis is very extensive and symbolisation has been done on some plan.

(2) The adoption of the same basic letter for a particular character in different crops is logical, as it is found that the genic effects may be similar when they concern homologous parts in different species.

(3) Multiple alleles are distinguished by gene symbols with superscript letters : *e.g.*, R, R^l, R^c, R^s, R^i, r^o for multiple allelomorphic series in Asiatic cotton anthocyan pigments.

(4) Complementary genes have the same common gene symbol with alphabetic subscripts, *e.g.*, C_{pa}, C_{pb} for crumpled leaf in cotton.

(5) Duplicate genes have the same common symbol with numerical subscripts, *e.g.*, Chl_1, Chl_2, for chlorophyll deficiency in new world cottons.

Symbolisation on these lines will ultimately enable a breeder to identify the character from gene symbol, *e.g.*, Chl stands for chlorophyll. From these symbols one can know the type of interaction involved in inheritance. This may be taken as a parallel instance to symbolisation of elements in chemistry such as O for oxygen, N for nitrogen and these symbols indicate the elements even in compounds. Gene symbolisation is on similar lines. Gene symbols for rice, cholam and cotton are given here for reference. (Vide Appendix IV).

Chapter 5

CELL DIVISION

THE CELL—CELL DIVISION—MITOSIS—MEIOSIS—DIFFERENCES BETWEEN MITOSIS AND MEIOSIS—CROSSING-OVER.

1. **The Cell.**—That living organisms are composed of cells was first discovered by Robert Hooke (1660) who, by examining a thin piece of bottle cork under the newly constructed microscope described the honey-comb-like structure as *cell.* In 1838–39 Schleiden and Schwann in Germany enunciated the *cell theory.* Theirs is one of the great generalisations of experimental biology. Both in plants and animals, the cell is not only the unit of structure but also of function. In 1831 Robert Brown discovered *nucleus* in the cell.

In 1861–62, Schultz and De Bary established the essential unity of protoplasm in all living beings. In 1875, Strasburger described the chromosomes and Hertwig proved that fertilisation consists in the union of two nuclei from the gametes. The discovery of Hertwig was useful in dispelling the doubts prevailing in those days regarding the role of the two sexes in sexual reproduction. These two authors in 1884–85, simultaneously identified that the nucleus plays an important role in heredity. In 1885–87 Weismann detailed the behaviour of chromosomes during cell division and predicted two types of divisions and in 1887–88 Boveri demonstrated reduction division in *Ascaris.* As a result of these two discoveries the importance of cell both in the structural and functional aspects of the organism became established. The single cell, the gamete, transmits all the hereditary characters from parent to the progeny. Before going into the details of cell division, the structure of a plant cell is outlined below.

The plant cell is surrounded by cellulose wall. The protoplasm inside the cell is differentiated into *cytoplasm, nucleus* and *plastids.* Nucleus is a dense body situated inside the cytoplasm. In the cytoplasm of plants are found discoid or spherical bodies termed plastids which bear pigments such as chlorophyll, xanthophyll and carotin. The plastids are responsible for transmission of plastid pigmentation from parent to progeny and thus cause *extra nuclear inheritance* of plant pigmentation in some cases, *e.g., maternal inheritance* of chlorophyll deficiencies.

The nucleus is dense and large when the cell is young and dividing. When the nucleus is not dividing it is termed the *resting nucleus,* a misnomer because, the nucleus is functionally always active whether dividing or not. The nucleus appears to be surrounded by nuclear membrane. There are one or more refractive bodies inside the nucleus and these are called *nucleoli.* During resting stage of the nucleus, the chromosomes are not visible due to their being in a hydrated state and having the same refractive index as that of nuclear sap.

At the initial stages of cell division the chromosomes begin to appear as distinct thread-like structures. Generally the number of chromosomes is constant in a species. However, different species may also have the same

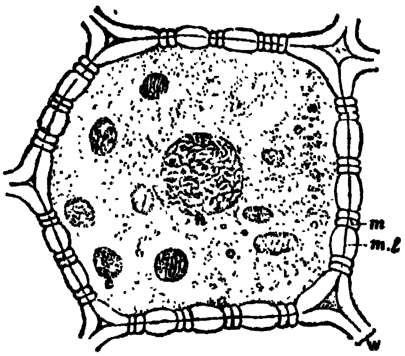


Fig. 30.—A typical plant cell.

chromosome number, *e.g.*, *Gossypium arboreum*, *G. herbaceum* (the cultivated Asiatic cottons) and *G. Stocksii* (the wild Asiatic cotton) show somatic number 2n—26. In a few cases the same species may show varying chromosome numbers *e.g.*, *Saccharum spontaneum.*

2. **Cell Division.**—In sexual reproduction the organism develops by the repeated division of the zygote. The latter divides repeatedly and in a human body there are about 10^{14} cells. There are intervals between the divisions and the interval may be short or long. In the course of repeated divisions all the hereditary materials remain constant without change and every somatic division results in equal distribution of the chromosomes between the two cells in such a way that the two daughter cells are identical with each other and also with the mother cell. This is made possible by the fact that each chromosome is longitudinally split into two chromatids and the split halves separate out. This type of cell division which takes place in the vegetative tissues is termed *Karyokinesis* or *mitosis* or *somatic division.*

Since the zygote results from the fusion of two gametes, there is doubling of chromosomes at the time of fertilisation. If each one of the gametes contains n chromosomes, the zygote contains 2n chromosomes. The zygote develops into a mature organism and again forms gametes for sexual reproduction. Weismann predicted and this was later confirmed that there must be a compensating division as otherwise at every fertilisation the chromosome number will be doubled. *Meiosis* or *reduction division* constitutes this compensating mechanism. The chromosome number in the gametes is half that in the plant body. It was already pointed out that sexual reproduction leads to great variations in the progenies while asexual reproduction causes no variation in the progenies. *Therefore meiosis is a contrivance by which the chromosomes show qualitative variation and are reduced to half the number during the formation of gametes.* In the flowering plants reduction division takes place when the pollen grains and ovules are formed. The pollen mother cells (PMC) and the egg mother cells (EMC) undergo reduction division.

3. **Mitosis.**—Mitotic cell division may be described under four distinct stages with regard to chromosome behaviour—(i) *Prophase*, (ii) *Metaphase*, (iii) *Anaphase* and (iv) *Telophase*.

Prophase.—It is indicated by coiled and contorted threads appearing in the nucleus. These threads which are chromosomes become increasingly "fixable" during prophase *i.e.*, when the cells are killed and stained by certain chemicals and stains, the appearance of fixed chromosomes approximates to that in living cell. The fixability of chromosomes is found to depend upon the colloidal hydration of the chromosomes. Belar showed that the chromosomes during the resting stage of the nucleus are highly hydrated and hence are not fixable ; whereas, during prophase, the chromosomes gradually get dehydrated and become increasingly fixable. The individuality of the chromosomes is maintained throughout the resting stage of the nucleus also. During the resting stage of the nucleus the chromosomes have split longitudinally and the two chromatids lie close to each other throughout their length and they are attached at the centromere.

Three changes are evident during prophase : (i) there is increase in the chromatin material of which the chromosomes are made, (ii) the chromosomse become shorter but thicker due to spiralisation of the chromosome thread, (iii) the chromosomes undergo dehydration. As the prophase advances, the chromosomes can be made out individually and they move to the periphery of the nucleus. The nucleolus slowly gets reduced in size and generally disappears at late prophase. It is found that a pair of chromosomes are attached to the nucleolus. These chromosomes are called nucleolar chromosomes and these are recognised at metaphase as satellites or secondarily constricted chromosomes. The function of nucleolus during cell division is not still clearly understood. It is believed that it contributes chemical material for the growth of the chromosomes. But it is now definitely established that the nucleolus is organised at telophase by the nucleolar chromosomes.

Metaphase.—At the end of prophase the chromosomes are found uniformly distributed in the nucleus. When metaphase follows, the nuclear membrane breaks down or the distinction of demarcation between cytoplasm and nucleus disappears and this stage is characterised by the appearance of *spindle*. From the two poles thread like bodies are seen to diverge towards the centre and these appear to be attached to the chromosomes at centromere. It should be remembered that there are no actual threads or organic attachment to the chromosomes. The spindle structure is explained to be a result of certain molecular rearrangement in the material of cytoplasm. At metaphase the centromeres of all the chromosomes arrange themselves in one plane at the *equator* forming *metaphase plate*. In this arrangement the distal ends of chromosomes may lie outside the spindle. The arrangement of the chromosomes at metaphase plate depends upon the number of chromosomes and their sizes. Generally the large chromosomes lie on the periphery while the smaller ones lie to the centre.

It was mentioned that the chromosomes appear as double threads at prophase. At metaphase the two chromatids lie very close to each other and

each of these chromatids are closely spiralised and therefore, by normal staining, the chromosomes appear like rods which are shorter and thicker than the early prophase chromosomes. Metaphase is the shortest stage in cell division. At late metaphase the centromere divides and the divided halves begin to repel each other. The chromatids separate out at the region of spindle attachment. The separation at this region is due to repelling force between the divided halves of the centromere and is not due to the action of spindle.

iii. *Anaphase.*—The chromatids begin to move apart and now they constitute *daughter chromosomes* (Fig. 31). In the initial stages of the separation of the daughter chromosomes there are no changes in the spindle but soon the region between the two groups of centromeres begins to elongate and form the *stem body*. This separates the two groups of daughter chromosomes which are now pushed to the respective poles. In this stage of cell division,

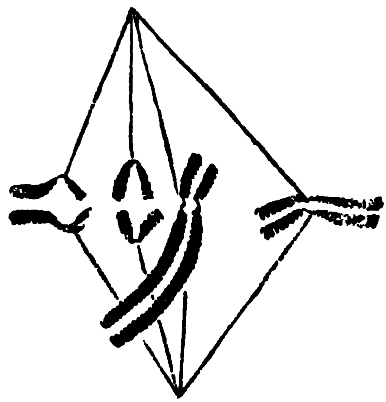


Fig. 31.—Early-Anaphase in mitosis. Note the attachment of chromosomes to the spindle at the region of the centromere.

each chromosome which was longitudinally divided but whose two halves were held close to each other, separates out the two halves to the opposite poles. As a consequence the daughter nuclei which are constituted by the two groups of chromosomes are identical.

Telophase.—When the two sets of daughter chromosomes—which by now assume the status of chromosomes—have sufficiently moved apart, the two poles disappear and a nuclear membrane begins to be formed round each group of chromosomes. A cell wall is formed between the two nuclei. Within the newly reconstituted nuclei, complex changes take place which in brief may be described as the reverse of changes taking place during prophase, *viz.*, the unwinding of the spirals, hydration and consequent unfixability.

In the telophase nucleus, the chromosomes are in single threads as they begin to change to resting stage while in early prophase of the succeeding division they appear as double thread. Naturally it is inferred that the chromosomes split in the intervening resting stage.

Mitosis may be summed up as the division and separation of identical halves of chromosomes into two identical groups from which the two daughter nuclei

are reconstituted (Fig. 32). The nucleus has divided into two without changes in the chromosome number or structure. A division in the chromosome is followed by a division in the cell.

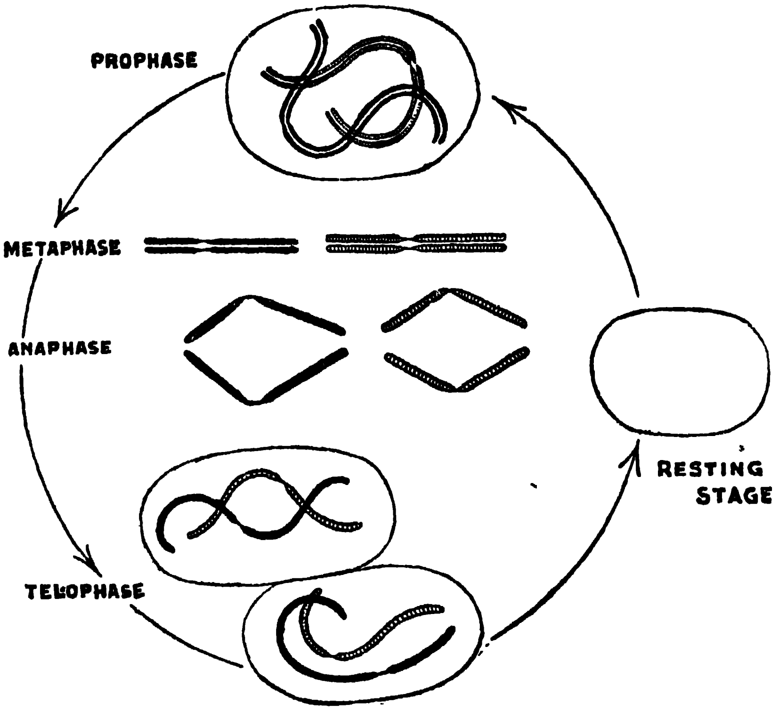


Fig. 32.—Diagrammatic representation of the different stages in mitosis.

4. **Meiosis.**—Briefly, meiosis may be defined as "*the occurrence of two successive divisions of a nucleus accompanied by one division of its chromosomes*". This reduces chromosome number to half the somatic number (n). This is an essential step in all organisms where fertilisation occurs in one stage of reproduction. The prophase of the first division is very much prolonged and consists of definite substages termed *leptotene, zygotene, pachytene, diplotene* and *diakinesis.* After a short resting stage, the second division takes place and this is like a normal mitotic division.

First Division.—The following is a brief description of meiosis in a diploid plant.

Leptotene.—After mitotic division the daughter cells which are to constitute the mother cell and undergo meiotic division start next division with very short resting stage. The chromosomes have not yet longitudinally divided and hence each chromosome consists of a single thread. In plants with especially long chromosomes the thread consists of a series of darkly staining minute granules '*the chromomeres*'. These granules or chromomeres are suggested to be the genes. These granules are of unequal sizes and lie at unequal distances in the thread which takes the stain faintly.

Zygotene.—The homologous chromosomes oome to lie side by side. Throughout their length the two chromosomes lie close to each other—they are said to pair. This pairing is strictly between homologous regions of the two chromosomes.

Pachytene.—Since the chromosomes are in twos, they are termed *bivalents.* In a cell with 2n chromosomes in leptotene stage there will appear *n* bivalents in pachytene. The two chromosomes coil round each other and this is termed *relational coiling.* The coiling is supposed to be due to internal torsion forces in the chromosome threads.

During this stage, the chromosomes divide longitudinally into two chromatids. The bivalents which appear in *two strands* at the beginning of prophase now appear in *four strands*.. At the four strand stage exchange of segments between the two members of a bivalent takes place. The exchange is between two chromatids only (one from each homologue) by breakage and re-union. This is termed *crossing-over.* If the two original homologous chromosomes are designated as ABCDEFGH and abcdefgh respectively, at four strand stage each gene occurs in double. If the segment FGH of one chromatid breaks, the corresponding segment fgh in the homologue also breaks and the broken ends rejoin to give rise to ABCDEfgh and abcdeFGH. As a result of crossing over, the four strands will be of the following constitution : ABCDEFGH, ABCDEfgh, abcdeFGH, abcdefgh. The first and the fourth represent the two parental types and the middle two represent new recombinations. When such exchanges have taken place the bivalents fall apart except at specific regions where they have broken and exchanged segments. These points of exchange, present a cross shaped appearance and are termed '*chiasmata*'.

Diplotene.—When the two chromosomes have split into four strands and when the exchange of segments has taken place by crossing over, the chromosomes begin to fall apart. This marks the beginning of diplotene stage. The separation of the chromosomes at diplotene is characterised by the appearance of chiasmata. The chromatids now begin to contract by spiralisation. The loops formed by chiasmata twist in such a way that alternate ones are in the same plane—just as the loops of a well stretched out chain. In some cases as the opening up of the loops of the chromosomes progresses, the chiasmata move from their original position towards the distal ends and away from the centromere and this movement of chiasmata is termed *terminalisation.* (Fig. 33).

Late diplotene stage is termed *diakinesis.* At this stage there is the greatest contraction of the chromosomes. The chromosomes are shorter and thicker than at the metaphase of somatic mitosis and especially in organisms with long chromosomes it is found that this is achieved by the formation of *major spirals.*

Metaphase.—The nuclear membrane disappears. Spindle is formed. The bivalents arrange themselves at the equator with the centromeres of each orientated along the axis of the spindle. It must be remembered that of the

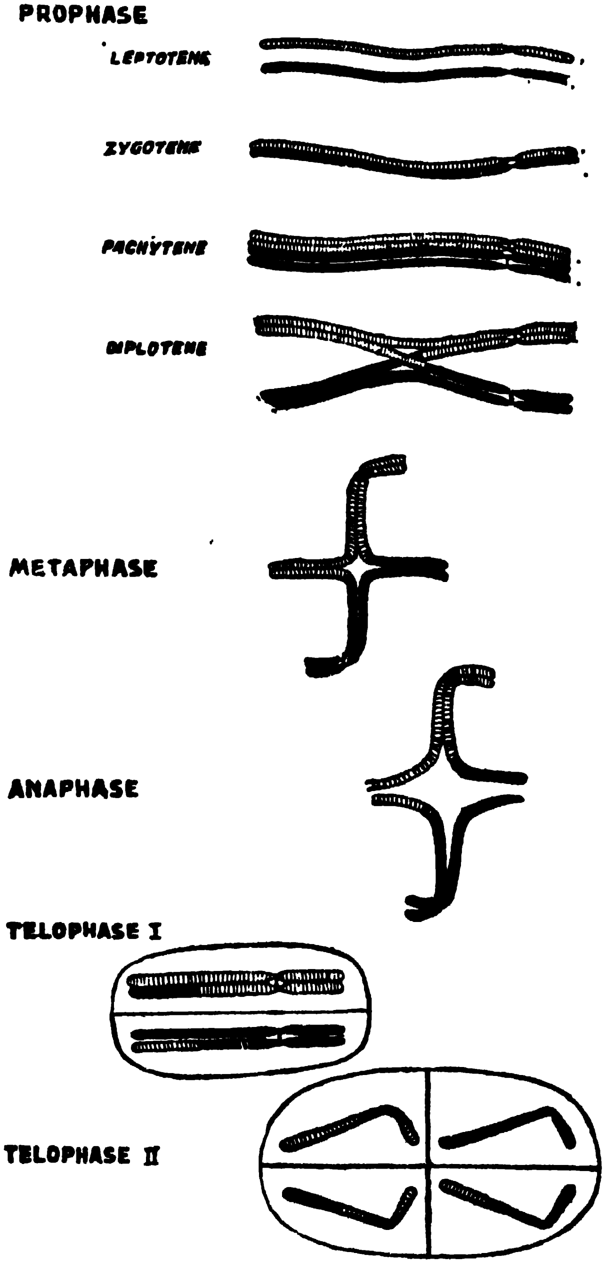


Fig. 33. Diagrammatic representation of crossing over between homologous chromosomes during meiosis. Note that at the end of Telophase II, a tetrad of four daughter cells are formed, two of which are parental and two recombined.

two members of the bivalent one is of paternal origin and the other of maternal origin. At the equatorial plane which of these be toward one pole or other is a matter of chance. The centromeres do not divide now. They hold the two chromatids together.

Anaphase I—At the anaphase I, the two centromeres of each bivalent repel each other. Each centromere moves along with it the sister chromatids into which the chromosome had already divided at pachytene. As already pointed out the separation of parental chromosomes in one bivalent is inde-

pendent of the separation in any other bivalent. For example if AA', BB' are two chromosomes of paternal origin, and aa' bb' of maternal origin, at anaphase I AA', aa' necessarily pass to opposite poles ; so also BB', bb' pass to opposite poles : but AA', BB' or AA', bb' may go to one pole. The assortment of the two chromosomes of each bivalent and their movements to one or the other pole is random. Further, the chromosomes of the bivalents are not the same as they were at zygotene stage as they have interchanged segments.

Telophase I.—The separated chromosomes are reconstituted into two nuclei which pass into *interphase*, *interkinesis*, or short resting stage. Two daughter cells or dyads are formed. This resting stage may be very short or may be even altogether absent. Each cell has haploid number of chromosomes.

Second Division.—The second division generally starts with a short resting stage after the first division. Prophase II when present is always very short.

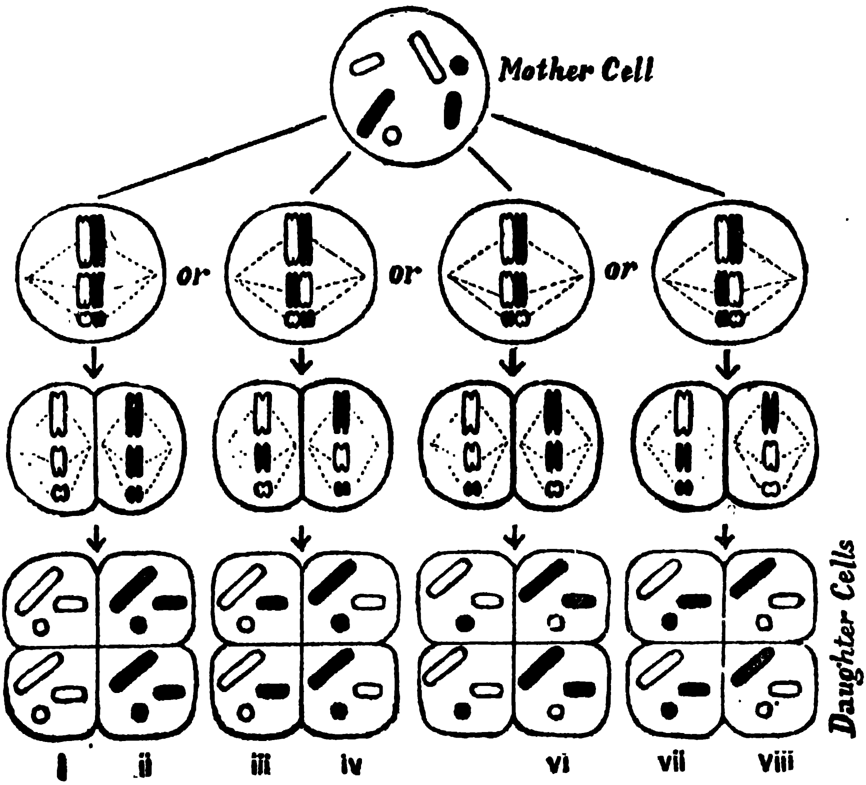


Fig. 34. The formation of 8 types of gametes from a mother cell with three pairs of chromosomes. *Note* the independent assortment of the three pairs of chromosomes.

The chromosomes at telophase I have not undergone any visible change during this resting stage. The second division is a normal mitosis. At metaphase II the nuclear membrane disappears, spindle is developed and the chromosomes lie with their centromeres in the equatorial plate. The sister chromatids lie loose along their length and are held at the centromere. There are only haploid number of chromosomes in each cell. The chromatids show

minor spirals only. At *anaphase II* the centromere divides and the two sister chromatids move to opposite poles. The movement and the separation of the chromatids are similar to the processes in normal mitosis. At telophase II, the daughter nuclei are reconstituted with haploid number of chromosomes in each.

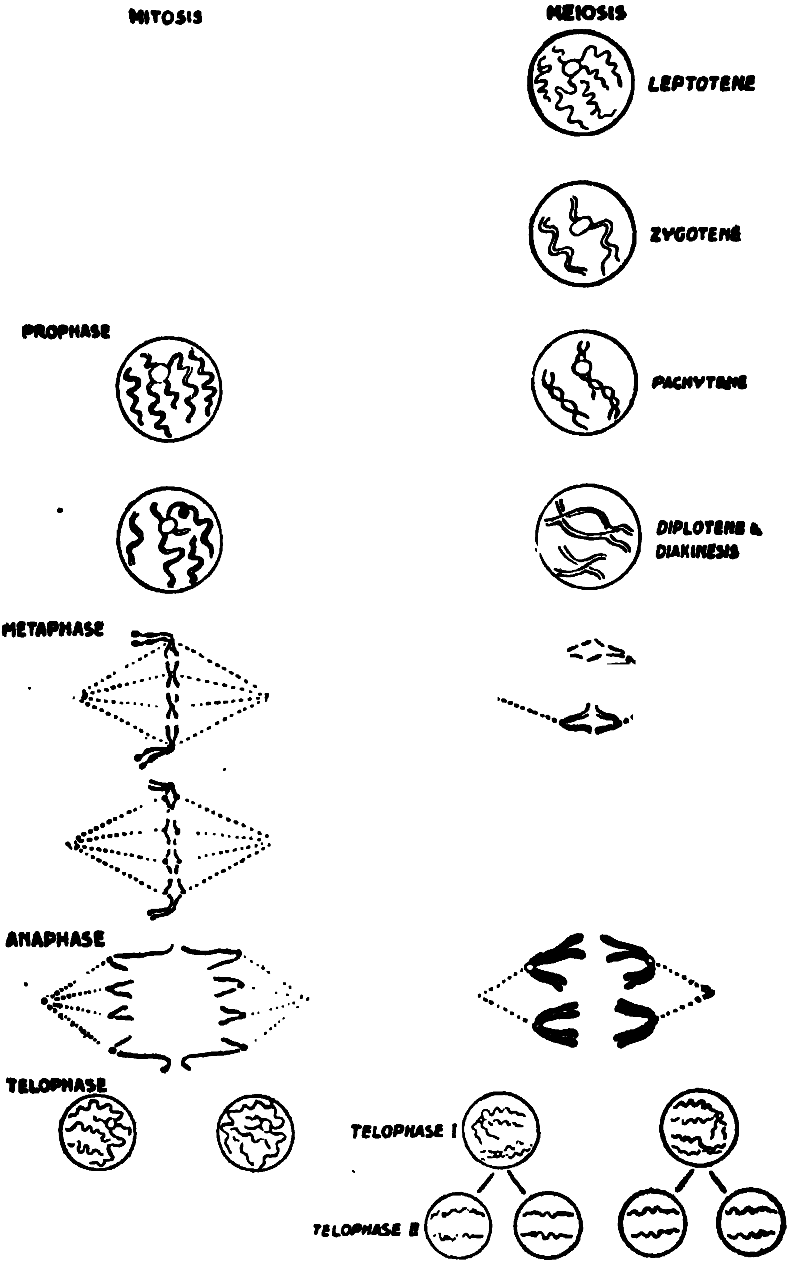


Fig. 35. Diagrammatic comparison between mitosis and meiosis. *Note* the prolonged prophase, crossing-over and the formation of tetrad with reduced and qualitatively changed chromosomes that characterise meiosis. The chromosomes at leptotene are not yet longitudinally split.

At the end of meiosis, each mother cell has resulted in four daughter cells termed *tetrad*. Meiosis in a mother cell with three pairs of chromosomes is illustrated in fig. 34.

5. **Differences between Meiosis and Mitosis.**—In essential features meiosis nd mitosis are alike and the former may be considered to be a modification of the latter. The two types of divisions have been described in detail and the differences between the same will be pointed out here. (Fig. 35).

Mitosis.	Meiosis.
(1) *Resting stage* preceding mitosis is long.	(1) *Resting stage* preceding meiosis is very short.
(2) *Prophase* is short without sub-stages.	(2) *Prophase* is prolonged with leptotene, zygotene, pachytene, diplotene and diakinesis sub-stages.
(3) The chromosomes are longitudinally split into two sister chromatids during the preceding resting stages. From early prophase they appear as double threads.	(3) The chromosomes are not longitudinally split but appear as single threads.
(4) The split homologous chromosomes are not attracted towards each other.	(4) At zygotene and the succeeding stages in prophase of first division, homologous chromosomes are attracted towards each other and they form bivalents. The chromosomes split into sister chromatids and at four strand stage, crossing over takes place. Exchange of segments of chromatids between the maternal and paternal chromosomes takes place. The chromosomes then fall apart with characteristic appearances depending upon the number and type of chiasmata.
(5) At *metaphase* the centromere of each chromosome divides and the sister chromatids move towards opposite poles. The somatic number is maintained.	(5) At metaphase I the centromere does not divide but the homologous chromosomes move towards opposite poles. The number of chromosomes moving towards any one pole is reduced to half the somatic number, *i.e.* reduction in the number of chromosomes has taken place.
(6) Each chromosome of paternal and maternal origin is longitudinally divided and the separation to opposite poles results in identical daughter cells at the end of mitosis.	(6) At metaphase I the orientation of chromosomes at the equatorial plate is such that either paternal or maternal chromosome only goes to one pole. The orientation in one pair is independent of the orientation in any other pair. The two daughter cells at the end of first division are thus not identical.
(7) The initial movement of the chromosomes at late metaphase is due to repulsion between the parts of divided centromere.	(7) The initial movement of chromosomes at late metaphase I is due to repulsion between the centromeres of homologous chromosomes.

(8) At anaphase further separation of chromosomes is due to the formation of stem body.	(8) At anaphase I the changes in spindle are the same as in mitosis.
(9) At *telophase* two daughter nuclei each with 2n chromosomes are reconstituted.	(9) At telophase I two daughter nuclei each with *n* chromosomes are reconstituted.
(10) There is no second division in mitosis. The daughter cells after varying periods of resting stage may undergo repeated mitotic divisions.	(10) There are two cell divisions for each meiotic division. The second division follows after a short resting stage. The second division is a normal mitotic division but with *n* chromosomes. At metaphase II, the centromeres divide and the sister chromatids are separated. This corresponds to metaphase of mitosis.
(11) At the end of mitosis neither the chromosome number nor the quality has changed.	(11) At the end of meiosis each cell of the tetrad contains *n* chromosomes and the quality of the same is changed.

In the resting stage between two mitotic divisions the chromosome is longitudinally divided. Meiosis starts after a very short resting stage and therefore the chromosomes have not yet longitudinally split by the time the prophase of first division starts. According to the *Precocity theory* of Darlington meiosis has evolved by precocious onset of prophase.

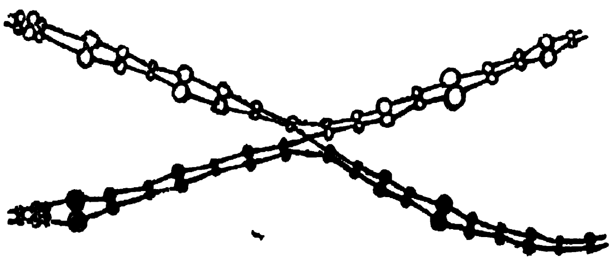


Fig. 36. Crossing over.

6. **Crossing over.**—The phenomenon of crossing over as it takes place during the pachytene *or early diplotene* is a very important one. It has been pointed out that the independent assortment of characters according to the second law of Mendel is due to the independent assortment of chromosomes at Metaphase I of meiosis. This assortment of chromosomes does not help in giving rise to a new combination of genes located on the homologous chromosomes. Crossing over is a physical step by which genes are exchanged between homologous chromosomes. It will be shown later that the number of cross-overs or chiasmata is not always the same in the mother-cells and neither do they occur at the same points of the chromosomes. The frequency and location are variable. (*vide* Chapter VII).

Chapter 6

CHROMOSOME THEORY

THE IMPORTANCE OF NUCLEUS—CHROMOSOMES AND CHARACTERS—PARALLELISM WITH MENDELISM—LINKAGE GROUPS—CROSSING OVER—CYTOGENETICS—CHROMOSOME STRUCTURE—CHROMOSOMES—BEHAVIOUR IN CELL DIVISION—GENES—SEX CHROMOSOMES—CHROMOSOME NUMBER IN PLANTS.

1. **The importance of nucleus.**—One of the primary characteristics of a living being is that it does not arise *de novo i.e.*, a living being arises from a pre-existing living being and it does not arise from the non-living. In the case of plants this reproduction may be sexual or asexual. In the case of asexual reproduction a part of the parent body gives rise to the new progeny. The role of male and female gametes in sexual reproduction of plants was recognised in the eighteenth century only. In either types of reproduction there is physical continuity between the parent and the progeny.

In the case of asexual reproduction such as in the planting of cuttings the physical continuity is evident, but in the case of sexual reproduction the physical link between the parents and the progeny is not easily discernible due to the microscopic size of the gametes, and hence people of the nineteenth century believed in spontaneous creation. The '*Cell-theory*' of Schleiden and Schwann (1838) and the principle of '*cell from cell*' enunciated by Virchow (1858) gave a blow to the theory of spontaneous creation. From thence, the cell became important from structural, physiological and hereditary points of view. Therefore the cell was studied in great detail between the years 1860 and 1900. It is now known that nucleus, the most important of the living constituents of the cell has continuity from generation to generation.

The cells multiply in number by division. Normally, a cell divides into two and form two daughter cells. Detailed observations have been made on dividing cells in recent times. During cell division, the nucleus is observed to undergo various changes and it plays a prominent part throughout the division. The nucleus appears granular during the resting stage. When it prepares to divide, during prophase, thread-like bodies begin to appear. Hofmeister (1848) detected these thread-like bodies but he did not attach any significance to them. It was in 1888 that Waldeyer coined the term '*Chromosomes*' for these thread-like bodies. These chromosomes constitute the prominent content of the nucleus. The importance of nucleus was slowly realised and as early as 1884 Strasburger, Hertwig and Weismann simultaneously detected that nucleus plays a role in heredity. Greater interest centered round the nucleus and particularly the chromosomes were studied in detail during cell division. In structure and function the chromosomes are definite and precise

and point to the possibility of their being the mechanism for heredity. The theory relating to the function of chromosomes as the physical basis of heredity is known as "*chromosome theory of heredity*".

Primarily the chromosomes arise by the division of pre-existing ones. The permanence of chromosomes is not only in regard to the number in a cell but also in their structure. Based on this, Weismann enunciated that "the permanence of physiological properties of organisms which is manifested in heredity is determined by the permanence in structure of their chromosomes." Thus the chromosomes in nucleus were suspected to be of importance in the inheritance of characters. *In* 1902, *Sutton pointed out the parallelism between Mendelism and the cytological behaviour of the chromosomes.* Further extensive studies of the chromosomes in relation to heredity showed beyond reasonable doubt that the chromosomes constitute the physical basis of heredity. The various facts which led to the acceptance of the 'Chromosome theory of heredity' are outlined in this chapter.

2. **Chromosomes and characters.**—If the chromosomes are carriers of genes which are responsible for the development of characters in living organisms, then there must be similarity between the behaviours of chromosomes and characters in heredity. To a large extent, the progenies resemble their parents. This happens generation after generation. Therefore large groups of individuals of common descent bear very close resemblance to each other. For example, if we consider the characteristics of the cultivated rice plants of the world, they all bear certain common characteristic features ; they resemble grasses in their general appearance, they exhibit tillering habit, internodes are covered by sheathing leaf bases, inflorescence is a panicle, the spikelets consist of two outer sterile glumes, the third one is fertile with hermaphrodite florets, six stamens, an ovary with plumose stigma and the fruit is a caryopsis enclosed in the persistent lemma and palet. Because the rice plants exhibit the characteristics of grasses, they are placed under *Gramineae*, and because all the cultivated rice plants resemble each other to a large extent they all come under one genus and species—*Oryza sativa*. But yet, the varieties of rice, cultivated in different parts of the world are distinct and differ from each other in a few minor characters. Similarly each plant within a variety is distinct from the other. This is a phenomenon common to all other organisms : *viz*., *groups of individuals (say species) exhibit certain constant and common characteristics and transmit the same to their progenies but yet the individuals differ among themselves. Therefore there are two tendencies in nature—one which preserves certain character groups and the other which permits variation.*

Observations on chromosomes have shown that the above phenomena are true in their cases also. Normally the chromosome number within a species is constant ; this constancy is true in respect of their size and structure. The chromosomes are directly derived from parents to progenies and therefore the chromosomes of an individual are but derivatives from those of their remote ancestors. Chromosome mechanics shows the possibility of small variations in chromosomes and this aspect is dealt with later in detail.

In addition to the gross resemblance between the character and chromosomal behaviour in evolution, certain direct observations on the individuals strongly suggest the same : e.g., the *sex chromosomes*. In organisms such as *Drosophila*, one pair of homologues shows unequal members. They are termed *xy* chromosomes and they are correlated with sex in the flies. The male flies show *xy* chromosomes in somatic cells and the female flies show *xx* chromosomes only. When gametes are formed, the male produces two kinds of gametes in equal numbers—those with *x* chromosomes and others with *y* chromosomes. The female produces only one type of eggs. On random mating, it is found that all zygotes with *xy* chromosomes develop into males and those with *xx* chromosomes develop into females. There are other types of sex inheritance which are dealt with later and in all the cases it is possible to correlate sex with particular chromosomes.

In the simplest form of inheritance, each character is represented by a factor in the gamete. On hybridisation, such characters do not blend with each other but behave as independent units. This is termed *particulate type* of inheritance. Chromosomes exhibit the same characteristics, *viz.*, they are also particulate in structure. Chromosomes are not homogeneous mass of chromatin with changing structure. Observations on well stretched out chromosomes show that they are constituted of discrete particles which are

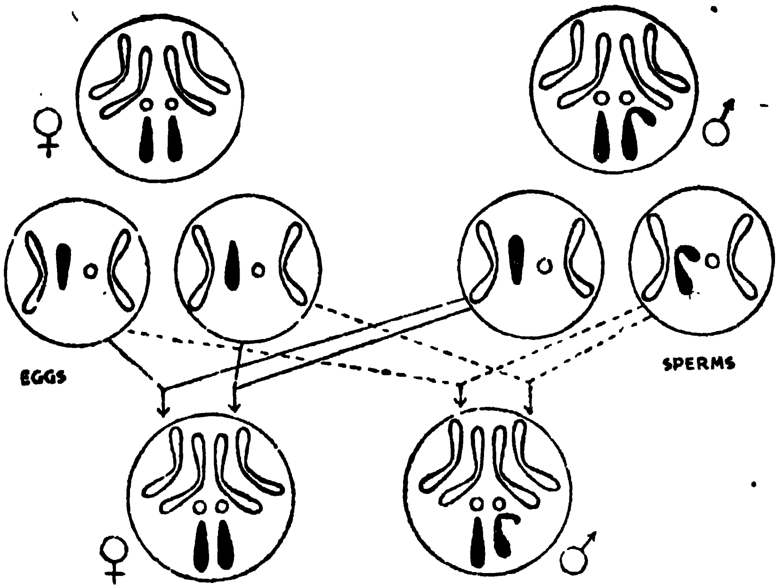
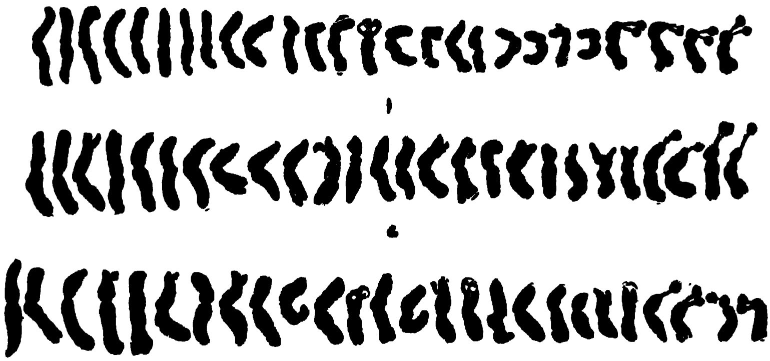


Fig. 37. Inheritance of sex in *Drosophila*. XX develop into females while XY develop into males.

permanent in form and occupy relative position on a particular chromosome. The first convincing evidence for this was from Wenrich (1916). In the grasshopper which he studied, certain chromosomes were recognisable by size, form and behaviour. He studied the chromosomes carefully and found that the chromomeres of each chromosome were definite in number size and

position. He traced one of the chromosomes in thirteen different grass-hoppers and found that the chromosomes from the different individuals were remarkably identical. Fig. 38 shows the morphology of chromosomes which characterise the three species of cotton.

Salivary gland chromosomes of *Drosophila* are found to be ideal for studying the structure of the chromosomes. In every cell the bands are of the same type and of the same sequence. Various experiments have shown the possibility of each band being correlated with the development of a character. Each band is in fact visual form of aggregates of similar genes or factors.



(With kind permission of India Government from I.J.A.S.).

Fig. 38. The chromosomes of three species of cotton. Top row :— *G. Stocksii.*—Middle row :—*G. arboreum Var neglectum forma indica.* Bottom row :—*G. herbaceum Var frutescens.*

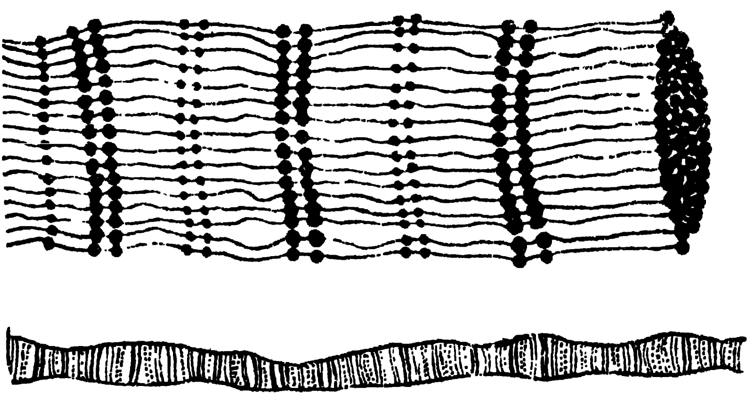


Fig. 39. Diagrammatic representation of salivary gland-chromosome.

Taking the case of plants, it is found that in all cases inclusive of the hybrids, *the offsprings derived by vegetative propagation are all identical, while the offsprings derived through seeds (except in perfectly homozygous types) are variable.* The vegetative propagation may be by cuttings, layering, budding, etc., from any part of the plant, *e.g.*, from a single Mulgoa mango tree, thousands of grafts may be prepared and all the graft plants will be identical with one another while seedlings from seeds differ widely. This points to the fact that vegetative buds on any part of the plant body are all alike but the seeds

differ genetically from one another. If it is assumed that the parent tree is a product of sexual reproduction, it has developed from a single celled zygote by a series of mitotic divisions. The identity of all the millions of somatic cells points to the necessity that mitosis results in identical daughter cells. In the case of seeds, which are the products of sexual reproduction genetical differences are evident because the gametes are all not identical. It is to be inferred therefore that maturation division or meiosis permits such differences to arise. Then it follows that *the chromosome behaviour in mitosis is parallel to character behaviour in vegetative propagation, and the chromosome behaviour in meiosis is parallel to character behaviour in sexual reproduction.*

In mitosis, the chromosomes at prophase are longitudinally divided. The centromere divides at metaphase and the sister chromatids are separated to the opposite poles. Since one half of each chromosome enters in the constitution of each daughter cell, the two daughter cells are identical with each other. Both paternal and maternal chromosomes behave alike and enter in the constitution of daughter cells.

Meiosis differs from mitosis as pointed out in the preceding chapter. At zygotene, the homologous chromosomes come together and begin to pair.

TABLE 16

Number of gene pairs. n	Types of gametes 2n	Permissible combinations in zygotes. 4n
1	2	4
2	4	16
3	8	64
4	16	256
5	32	1,024
6	64	4,096
7	128	16,334
8	256	65,536
9	512	262,144
10	1.024	1,048,576
11	2,048	4,104,304
12	4,096	16,777,216
13	8,192	67,108,864
14	16,384	268,435,456
15	32,768	1,073,741,824
16	65,536	4,294,967,296
17	131,072	17,179,869,184
18	262,144	68,719,476,736
20	524,288	274,877,906,944

The identical chromomeres come together. At the four strand stage of the pachytene the chromatids of paternal and maternal origin break and cross-over. It was also pointed out previously that the cross-overs do not occur at the same point. As a result of crossing over, random exchanges between maternal and paternal chromatids take place. On account of this, the millions of gametes from a hybrid are all different from one another. Random mating between

the gametes vastly increases the possible number of variations that can arise by sexual reproduction as shown in table 16.

By theoretical calculations it is surmised that there may be about 5,000 gene pairs in *Drosaphila.* It is much greater in complex organisms like man. Therefore, the type of gametes and the possible gametic combinations run to astronomical figures. Actual counts of the cross bands in the salivary gland chromosomes is a pointer to the same possibility.

Genetical studies have shown the role of the two parents in their contribution to the characteristics of the progeny to be equal. Observation under microscopes show that this relationship holds good in respect of chromosome contribution by either of the parents. The zygote cortains one haploid complement of chromosomes from each parent. The male and female gametes show equality in respect of chromosome content only and they differ in respect of their contribution of cytoplasm in the formation of zygote. Generally, the egg contains large bulk of cytoplasm and the sperm carries very little of the same. In spite of this, it is found that only the nucleus has a major role in heredity.

3. **Parallelism with Mendelism.**—The chromosome and character behaviours resemble each other closely not only in respect of general features as outlined above but also in respect of Mendelian phenomena of segregation and independent assortment. Mendel assumed that the factors are present in somatic cells in duplicate while they are single in gametes. Parallel to this, the chromosome number in somatic cells is double that in the gametes. According to Mendel the reduction takes place at the time of formation of gametes and meiotic cell division takes place only when gametes are formed. Mendel further pointed out that even though the factors are co-existent in heterozygous state, their character expression in later generations is not altered, *i.e.*, the individuality of the factors is maintained. Parallel to this, at fertilisation, the fusion of the nuclei results in the coming together of the two chromosome complements in the zygote and their individuality is never lost either at the time of fertilisation or later in the course of further growth and development of the zygote into an adult organism.

In Chapter III, the mono and dihybrid ratios were explained by locating the factors on chromosomes. The independent assortment of chromosomes at anaphase I of meiosis is a physical phenomenon observable under microscope. Carothers (1913) actually demonstrated this for the first time in the grasshopper *Brachystola.* The x-chromosome did not divide at the first division of meiosis but moved to one of the two poles. The two cells of the dyad are recognisable in this case by their size difference. The association of the x-chromosome with the smaller or larger component was found to be a matter of chance. Later observations on the assortment of recognisable members of homologous chromosome pairs confirmed the hypothesis that the paternal and maternal chromosomes assort themselves on random basis at the first meiotic division. The parallelism between Mendelism and chromosome behaviour in cell division was first noted by Sutton (1902) and this may be summarised in the following table 17.

TABLE 17.

Mendelian Factors.	*Chromosomes.*
(1) The factors in somatic cells are double in number as compared to the gametes.	(1) The chromosome number in somatic cells is double in number as compared to the gametes.
(2) The two members of an allelomorphic factor pair remain together in F_1 but segregate when gametes are formed.	(2) The two parental chromosomes remain together in the F_1 but separate and pass to the different gametes.
(3) When two pairs of factors are involved in a cross, they segregate independent of each other.	(3) When two pairs of homologous chromosomes are considered during cell division, the separation of the two members of any one pair is independent of separation in the other pair.
(4) The individuality of the factor is maintained generation after generation.	(4) The chromosomes of an individual are directly derived from its parents and the individuality of the chromosomes is maintained at all stages of development of the new generation.

4. **Linkage groups.**—The independent assortment of factors is not found true in all cases, but very often particular groups of factors are found to go together. These factors are then said to be linked and this phenomenon of *linkage* is discussed in greater detail in the next chapter. Morgan assumed that the *linked factors are all situated on the same chromosome.*

If it is assumed that all factors are located on chromosomes only and that the factors on any one chromosome are linked, it follows that the number of linkage groups should not exceed the haploid number of chromosomes. This is termed the "limitation of linkage groups". By genetical studies the number of linkage groups has been estimated in a number of organisms and in all these cases the haploid number of chromosomes corresponds to it. For example, more than 350 genes of *Drosophila melanogaster* have been studied and they all fall into four linkage groups, and there are only four pairs of chromosomes ; in *D.virilis* there are six pairs of chromosomes and six linkage groups ; *D.willistori* there are three large chromosomes and three linkage groups. In plants such as maize, peas and snapdragon, the number of independently assorting character pairs is the same as the number of chromosome pairs. The linear arrangement of chromomeres has been already referred to. If a linkage group comprises of a large number of characters, the corresponding chromosome must bear large number of chromomeres. Such a chromosome must be longer than the one with few chromomeres representing a smaller linkage group. This is actually observed to be the case. Large chromosomes represent large linkage groups.

5. **Crossing over.**—Linkage may not be so complete as to prevent even a few recombinations to appear in F_2. As a consequence recombinations in F_2 are not according to expectations in that the parental forms are in excess. Recombinations in such cases is explained by the crossing over that takes place at the pachytene. A definite proof for the relationship between crossing over at meiosis and the recombination of factors in F_2 was furnished by Plough's (1917) experiments on *Drohopsila.* This phenomenon is further discussed in the next chapter.

6. **Cyto-genetics.**—The fact that the chromosomes are carriers of heredity has led to the study of chromosomes to find out explanations for complex breeding behaviour of the individuals. There are many instances where breeding behaviour has been explained on the basis of cytological observations made at meiosis. For example, sterility in the interspecific hybrids *Gossypium anomalum* X *G. arboreum*, *Brassica nigra* X *B. campestris*, etc., has been explained on the basis of non-homology and consequent non-pairing between the two chromosome complements ; semisterility in rice was explained on the basis of segmental interchange. When the somatic chromosome complement is doubled artificially, the plant exhibits corresponding changes in phenotype and breeding behaviour.

The two parallel studies, *viz.*, cytology and genetics, which progressed on parallel lines were unified into *cyto-genetics* in the first decade of this century. Cyto-genetics gives complete picture of the mechanism of heredity. The principles of heredity, as well as behaviour of chromosomes are fundamentally the same in both plants and animals. Any change in the chromosome, either in number or structure, means a change in the genotype ; the change in the genotype is mostly reflected in the phenotype. The genotypic change may concern morphological or physiological characteristics with small or large visible effects.

In plant breeding, hybridisation between closely or distantly related plants has been largely attempted and many difficult situations have been met with. The solution to these by further genetical analyses may involve time and energy ; in these instances cytological observations quickly yielded the required informations. The structure and behaviour of chromosomes in the cultivated crops and their wild allies are now found to be very important to plant breeders.

7. **Chromosome structure.**—Chromosomes are thread like bodies showing beaded appearance. The beads represent the genes and are termed *chromomeres.* These beads are arranged in a linear fashion and the arrangement is constant from generation to generation. Any change in the arrangement may lead to change in the phenotype and genetic behaviour of the organism. In a resting nucleus, the chromosomes do not appear as distinct bodies but when the cell prepares to divide, the chromosomes become distinct. On this score it was once contended that the genes are set free in a resting nucleus and that they re-assemble before the nucleus begins to divide. There are various difficulties if this hypothesis is accepted. It has been pointed out that the genes located on the same chromosome are linked and the linkage intensity between the characters is constant from generation to generation indicating that the same set of genes are located in a given order on any chromosome. If genes are let loose in a resting nucleus, they must be presumed to possess extraordinary capacity to re-assemble to form the constant grouping of the species and also come together in a particular order. Observations do not justify the assumption of such specific attraction between different genes on a chromosome. There is another cytological evidence against this hypothesis. The chromosome at the preceding telophase and the early prophase of the following

division are exactly like each other in respect of their appearances and spirals. Kuwada showed that by exposing the nucleus of a dividing cell, the nucleus can be transformed to simulate a resting nucleus. This emphasises the fact that the difference between the resting and dividing nuclei is only a matter of their physical state. In mitosis the threads are re-duplicated while in meiosis they are not. The chromosome structure is therefore constant in a normally breeding population and any change in chromosome structure has its repercussions on phenotype or breeding behaviour.

The chromosomes in many cases are very small and except in the salivary gland chromosomes of Drosophila, no observations regarding chromosomes can be made. Since the chromosome structure is recognised as important, morphological observations such as size, shape, constructions, etc., of chromosomes have been recorded. However, the morphology of the chromosomes regarding size, length, the position of the centromere and satellited or secondary constricted chromosomes could be studied in relation to the changes that may occur in different species.

According to the position of the centromere the chromosomes are morphologically classified as *median*, *terminal* or *subterminal*. Combined with the description regarding the length of the chromosome, such as long, medium and short the chromosomes are described as follows :—

Sub-median, medium long : *e.g.*, second and third chromosome of *Drosophila*.

Submedian, short chromosome : *e.g. Commelina bengalensis*.

Chromosome with long secondary constriction *e.g. Rhoeo discolor*.

The constrictions are always intercalary and never terminal.

8. **Genes.**—The organism as a whole, the cell as a whole, the nucleus, the chromosome, the genes and centromere can arise only from the pre-existing ones and cannot arise *de novo*. While the protoplasm shows properties of living as opposed to inert matter like protein molecule, *the gene which is also suspected to be a complex protein molecule not only appears to be a living matter but shows a high capacity to organise complex physiological and developmental changes which are specific properties of these*. Mendel supposed that there is ' something ' in the germ plasm which represents the character of the adult and this was later variously termed as factor or gene. Cytologically, the banding which is observed in the salivary chromosome of *Drosophila* is taken to represent the factor or gene and such banding is supposed to be present in all chromosomes. Genes are situated on chromosomes and one seems to be separated from the other by non-genic material. The genes are of the size of big protein molecule. Calculations show that in a simple fly like *Drosophila*, where the haploid number of chromosomes is four, there are as many as 5,000 to 6,000 genes but the estimates arrived at by different calculations widely vary, and it is suspected that there may be even as many as 10,000 genes in that simple organism.

Regarding the chemical nature of a gene, it is believed that it is of the nature and similar to " polypeptide links." The chromosomes are not homo-

geneous in structure and this is to be expected from the banded structure of the salivary gland chromosome. Bridges computed that there are about 2650 bands in the salivary gland chromosome of *Drosophila.* It is further computed that the diameter of a gene may be about 20 $m.\mu$. and the volume about 4190 c. $m.\mu$. The banded region is darkly stained and the intervening space is not so much stained. The behaviour of centromere at the time of cell division shows that it is differently constituted from the rest of the chromosome.

Gene exhibits two important characteristics :

(1) it is autocatalytic, it reproduces a gene exactly like itself. Probably this is performed not by a split in the existing gene but by actual reconstruction of a new gene by its side.

(2) By its complex activities the gene sets up reactions outside the nucleus. These reactions may be resembling those of enzymes or hormones. These ultimately cause certain specific qualities to be developed by the organism. The exact nature of the reactions is not yet understood.

Stanley (1935) showed that the tobacco virus is a large protein molecule with certain properties of protoplasm also. This is an important link between the living and the non-living and the protein molecule of the virus shows the power for autocatalysis. The progenitor of the gene is probably similar in its origin. Hurst (1932) even suggested that the gene might be the original living substance.

Genes, in their action, may control the quantity of substance produced or the pattern of development. They are accordingly arbitrarily termed *substance genes* and *pattern genes.* The various steps by which a gene goes into action for developing a character is not yet clearly understood. Embryological and tissue transplantation studies in insects showed the possibility that the development is predetermined in egg itself. This gave rise to controversies between the " *pre-formationists* " and the " *epigeneticists* ". The former held that all the adult characteristics are there in the egg itself and only requires to be unfolded in the course of development of the organism. The latter held that it is purley a matter decided in the course of development. It is now known that the genotype of the egg permits a certain limited number of reactions to occur and this may be taken as " preformed " ; but in the course of development the genotype reacts with the environment and the development may be turned into alternative channels to give different phenotypic results. Thus the phenotypic differences between two organisms may come to depend on the differences in the genotype or it may be due to the effect of different environments acting on the same genotype. Reference to **phenocopies** and Bonnier's transplant experiments may be made in this connection. Our knowledge of the mechanism of development and to what extent the different steps are gene controlled is not clear. Even in the case of phenotypes showing single gene difference, the developmental processes are complicated. Genetic control of flower colour variation showed that the colour effect is produced by (1)

variations in cell sap pH and (2) production of co-pigments which are colourless but when added to anthocyanins produce colour. In certain cases all the substances may not be produced in the organ itself but some of them may diffuse from the neighbouring tissues. Thus in *Drosophila* it was found that in pigment development in eye the action of gene may be limited by such diffusion of substances.

A single gene may control a complex of development such as stature *e.g.*, dwarfing in cholam was due to mutation of a single gene or the gene may affect physiological reactions such as in the case of ageotropic mutant in paddy. The alternative courses of development open to a gene, may be exhibited by gene mutation or by the effect of environment. In cotton, the petalody mutant is an example, where the stamens are changed to their homologous organs *viz.*, petal. In the same crop, a mutant for leaf form—crinkled leaf (6133)—showed the mutant character in normal season while a few normal leaves developed late in the season. The measure of frequency of expression of a gene is termed *penetrance*.

Even though a character is governed by a single pair of genes, from the development point of view, many steps may be involved. That a character is monogenic in inheritance does not mean that the development of the character is by a single step. For example, the pericarp colour in *Eleusine coracana*, green and light green, differed by a single factor-pair (Cx-cx) and histological studies showed that the two characters differed in the number of chloroplasts in each cell and the size of chloroplasts as shown below :—

	Deep green.	Light green.
Chloroplast per cell	14	7
Size of chloroplast	7.6 μ	5.5 μ

A single gene may affect a number of distinct characters when the phenomenon is said to be *pleiotropism* and the gene as *pleiotropic*. This has been noticed in a number of cases.

In *Lupinus* a factor for red flower colour increases the height of plant from 60 to 69 cm and also causes development of anthocyanin pigment in vegetative parts. Glabrous and shiny seed coat is also developed by the same factor. Hallquist (1921) classifies pleiotropism into *isophase* and *heterophase*. In isophase, the gene has similar effect on several characters and in heterophase the reactions are opposite in type. Gruneberg (1938) classified pleiotropism under three heads :—(1) Caused by direct action of the gene but with different methods, (2) Caused by the direct action of the gene with the same method (3) direct action with subordinate effect. The Punjab hairy lintless gene is a good example for pleiotropism. The Punjab hairy lintless mutant gene l_{lc} and its allelomorph L_{lc} affect linted-lintless characters, height, boll size, fertility, number of ovules per lock and also viability of the seed. The action of the gene is more pronounced in the reproductive phase of the plant. Detailed studies showed that reduced viability of seed, reduced number of nodes in the plant and reduced ovule and seed number are by direct action of the gene but by different methods. Height of plant, length of internodes, size of bolls

and length of leaf lobe fall into Gruneberg's second group. Lint development falls into third group since the differentiation of hair initials is not affected but the action of gene in the course of development brings about the differences. While the gene affects the general growth from the beginning, its effect is more pronounced at the reproductive phase of the plant.

The gene, in its course of developmental reactions, may have alternative courses not only forced by external environment, but also the rest of genotype may influence it. The expression of a gene in different genetic back grounds is not the same. This may be exemplified by Harland's work on "crinkled dwarf". The mutant crinkled dwarf frequently occurs in *Gossypium barbadense* and it proved recessive to the normal in that species. When the same gene is transferred to *G. hirsutum*, in which species the mutant was not observed, it proved to be intermediate to normal. This is further confirmed by the phenomenon "position effect", which was studied in *Drosophila* by Sturtevant. The development depends not only on the rest of the genotype but also on the position of the gene. When the normal gene is duplicated, it causes reduction in the number of facets in the eye of the fly. This is termed 'bar eye'. Unequal crossing-over causes three genes to be in the homologue and this results in 'Double bar eye' (Fig. 40).

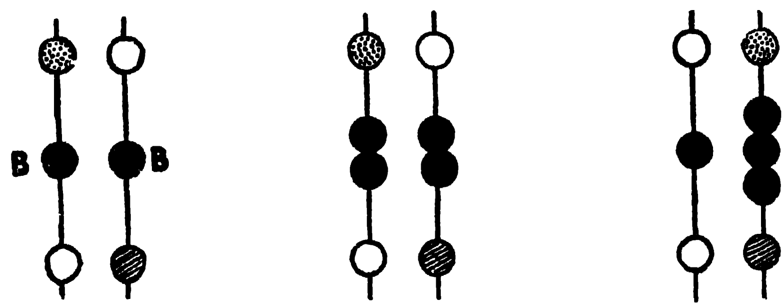


Fig. 40. Position effect of genes. B causes normal eye. BB causes 'bar eye.' Unequal crossing-over as shown in the right extreme causes 'Double bar-eye.'

This shows that in the expression of a gene not only the genotype as a whole is to be considered but also the genes in the neighbourhood have influence. It is therefore seen that the gene is specific in its action and depends upon the genotype and environment for its expression.

9. **Sex chromosomes.**—Plants and animals reproduce sexually, though in the former asexual methods are also widely present. In higher animals reproduction is bi-parental, *i.e.*, the male and female sexes are in separate individuals. In plants, both the sexes may be in the same flower (hermaphrodite), in different flowers but on the same plant (monoecious), or in different plants (dioecious). In the case of animals, the two sexes differ in many *primary and secondary characters.* The differences between the sexes are sharp and the variation from one sex to the other is discontinuous. There must be some mechanism by which such discontinuous variations could arise with great regularity. Since hereditary characters are represented by genes in the chromosomes of the gametes, the inheritance of sex must be sought in the chromosomes of the two sexes.

Investigations of Wilson (1905) threw the first light on sex chromosomes. In all organisms, the somatic cells contain chromosome in pairs and it was found that the two members of one of the pairs were different in form, *i.e.*, *heteromorphic*. The heteromorphic pair in male *Drosophila* is designated XY and the corresponding homologue in the female is XX. The inheritance of sex is schematically shown in Fig. 37.

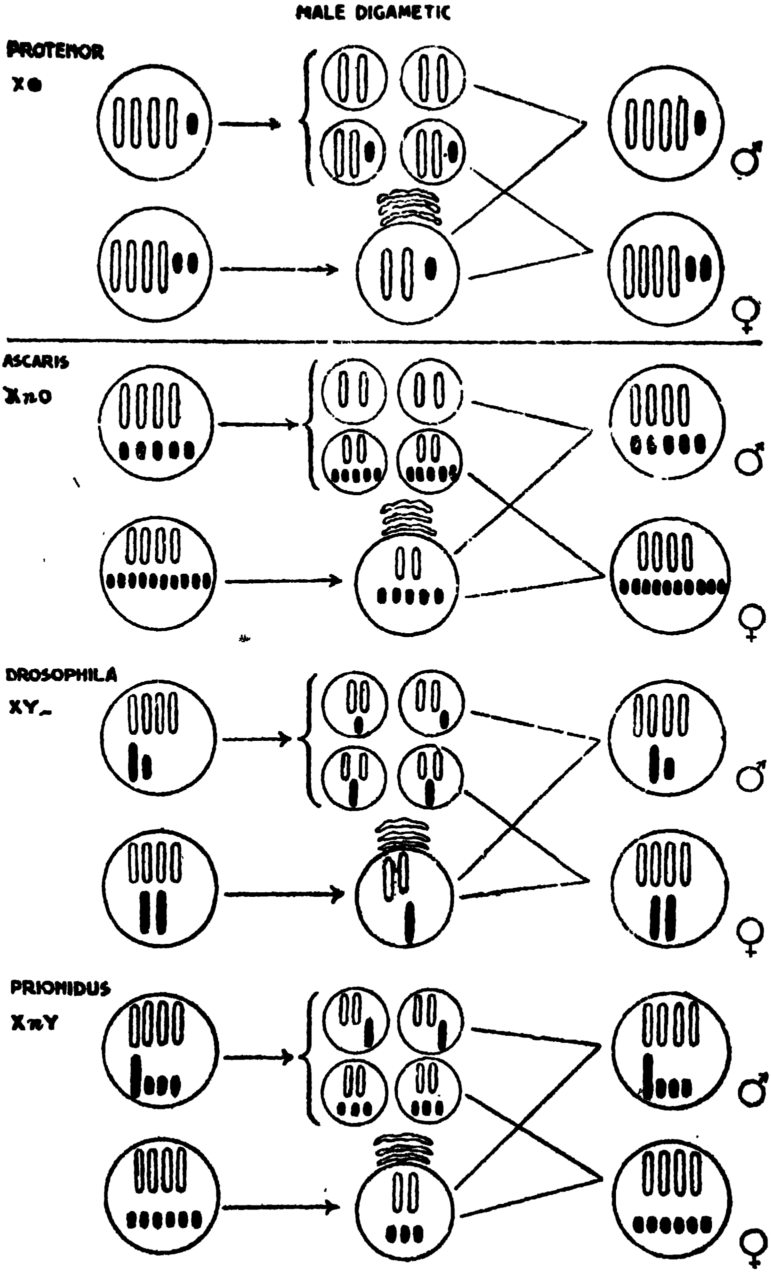


Fig. 41.—Types of sex chromosomes. The males produce two types of gametes and the females only one type.

Variations in y have been noted and in some forms y is entirely absent so that the female is XX and the male is XO, e.g. *Trimerotropis.* X and Y chromosomes are termed as *sex chromosomes* while the remaining pairs in the cell are termed *autosomes.* The work of Goldschmidt on *Lymantria* shows that sex is not only qualitative but also quantitative in that a series of grades between the two sexes termed *inter-sexes* were possible.

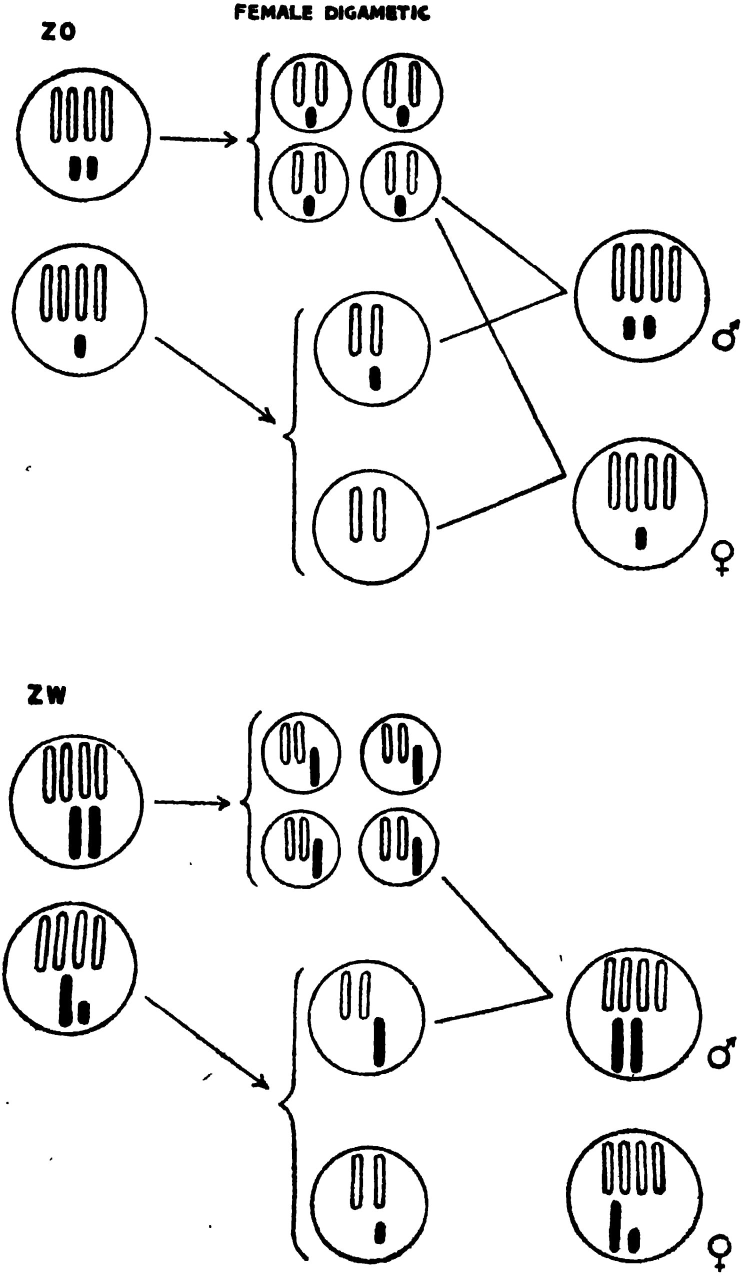


Fig. 42.—Types of sex chromosomes. The females produce two types of gametes and the males only one type.

In certain moths, birds, fishes and in straw berry family the male is homozygous (ZZ) and the female is heterozygous (WZ) and this is the reverse of XX-XY scheme of sex.

In some organisms, the male is heterozygous in respect of the sex chromosomes and in others the female may be heterozygous. The various types of male and female heterozygosity is summarised in Figs. 41 and 42.

The general theory of sex determination as postulated by Goldschmidt and others, states that every individual contains both masculine and feminine elements. If the masculine element is predominant then the individual is male. Morgan thinks that the balance between the masculine elements of autosomes and the feminine elements of x-chromosomes decides sex. Kosswig assumes that in fishes, the masculine elements are located in y chromosome and the feminine elements are in autosomes. x-chromosome in this case is taken to be empty or *inert*. It is also assumed now that the sex-chromosomes are convertible into autosomes or *vice versa*. In some cases such as *Pseudococcus*, the chromosomes from the male and female parents keep separate and here all the chromosomes behave as sex chromosomes. In bees, wasps, etc., unfertilised eggs develop into males and hence the latter are haploids and the fertilised eggs develop into females and hence the latter are diploids.

Therefore sex differentiation is now known to be not only qualitative but also quantitative and all grades between the two sexes are possible in some cases at least. The location of male determining sex genes may be in x or y chromosome or in some cases the balance between the sex chromosomes and autosomes may decide the sex.

10. **Chromosome number in plants.**—The chromosome number in different plants have been extensively studied. From the genetical studies discussed so far, it is clear that the chromosome number by itself is no sure guide either to the genetical behaviour of an organism or to its relationship to others. A perusal of the chromosome numbers of the various flowering plants shown in the appendix shows that unrelated plants may show the same chromosome numbers, *e.g.*, paddy and brinjal show $2n=24$. However, within certain limitations the chromosome number of crop plants provide valuable indications to a breeder. These will be discussed in a later section. For easy reference, chromosome numbers of a few important plants are listed in appendix.

Chapter 7

LINKAGE

INTRODUCTION—LINKAGE IN F_2 DATA—GAMETIC PROPORTION—CROSSING-OVER—CALCULATION OF F_2 RATIO—LINKAGE INTENSITIES—IMPORTANCE IN BREEDING—SEX LINKED CHARACTERS—LINKAGE VALUES IN CROP PLANTS.

1. **Introduction.**—According to Mendel's second law, factors assort and recombine independently in the F_2 generation and when two pairs of factors are involved a phenotypic ratio of 9 : 3 : 3 : 1 is obtained. Extensive experiments on both plants and animals showed that in a number of cases *not all the parental characters do recombine independently but in many cases either the recombinations do not appear at all or they appear in smaller frequencics than expected.* Such a phenomenon where the recombination between factors is reduced is explained as due to *linkage* and this was already referred to in the preceding chapter. The first instance to be noted was by Bateson and Punnett (1906) in sweet peas. The two pairs of characters involved in their cross are purple flowers with long pollen grains. Purple was dominant over red and long dominant over round. The F_2 phenotypic ratio did not conform to 9 : 3 : 3 : 1 expectations, but the parental types were far in excess of expected figures while the recombinations—purple flower with round pollen or red flower with long pollen—were few. Such linkages are found to be common in both plants and animals.

2. **Linkage in F_2 data.**—The following is an example of linkage reported in cholam.

Fully feathered stigma (*Stbf*) is a monogenic dominant over basal feathered stigma (*stbf*) ; Awnless (*A*) is dominant over long awn (*a*). The parental type which is fully feathered and long awned was crossed with another which is basal feathered and awnless. F_1 showed the dominant characters.

On segregation the following proportion of phenotypes was observed.

TABLE 18.

	Awn nil.		Awn long.	
——	Stigma fully feathered.	Stigma basal feathered.	Stigma fully feathered.	Stigma basal feathered.
(1)	(2)	(3)	(4)	(5)
Observed	549	248	263	11
Expected on 9 : 3 : 3 : 1 ...	603	201	201	67
Expected on 20% cross-over gametes.	546	257	257	11
	Recombined type.	Parental.		Recombined type.

Though recombined forms shown in columns 2 and 5 have appeared in F_2 they are far short of expected numbers on the basis of 9 : 3 : 3 : 1 ratio. *The parental forms appear in excess of expectation.* Therefore, the genes *Stbf* and '*a*' tend to remain together and the tendency for *Stbf* to combine with *A* or for *stbf* to combine with '*a*' is less than normal. Of the two parents involved in this cross, each parent is individually responsible for one dominant and one recessive factor. Linkage in such crosses is said to be in *repulsion phase.* There are instances where, the two linked dominant factors may be present in one parent and the two recessive factors may be present in the other. Linkage in such crosses is said to be in *coupling phase.* The terms coupling and repulsion have lost much of the significance with which they were originally used but yet they are used to indicate the parental types entering the cross. It should not be understood to mean any actual attraction or repulsion between the factors concerned. In both the cases the basic phenomenon is the same.

In his genetic studies on *Drosophila*, Morgan found linkage between many characters. He explained linkage on the basis of chiasmatype theory. According to him the *genetic factors are linearly arranged on chromosomes and the factors located on the same chromosome are linked. The less is the distance between two factors on a chromosome the greater is the linkage between them ; i.e., recombination between the two factors is far fewer than between more distantly located factors. Therefore the percentage of recombinations is a measure of linkage : the greater the linkage, the smaller is the percentage of recombination : the more loose is the linkage, the larger is recombination percentage.* On this basis, the relative distance between the various factors on a chromosome are estimated. By studying the inheritance of a large number of characters in *Drosophila*, Morgan and his collaborators calculated the linkage values for the factors situated on the same chromosome. By this method, the relative positions of the factors on the four chromosome pairs of the organism were located. Maps representing the four chromosomes and the position of the various factors or genes on them were constructed. These maps are termed *chromosome maps*. In the preceding chapter it was pointed out that the number of linkage groups is the same as the number of chromosome pairs. In an organism like *Drosophila* with four pairs of chromosomes, *the maximum number of groups of characters that can follow Mendel's law of independent assortment is only four. Any group of five pairs of characters must necessarily show linkage at least between two of the five. Similarly, in Ascaris with n-2, only dihybrid ratio can be expected and no three factors can assort independent of each other.* Another evidence for the limitation of linkage group comes from 'tubby' fly in *Drosophila melanogaster.* This fly has shortened body and bulgy eyes. The factor for 'tubbyness' did not fall into any of the known four linkage groups of normal flies and that factor behaved independently of the four groups of linked characters. Cytological examination showed that this fly had a chromosome fragment in addition to the normal complement of four chromosomes.

3. **Gametic proportion.**—Since the phenomenon of linkage is concerned with recombination of genes the explanation for the same must be sought in meiosis and the formation of gametes. It was previously shown that the gametes of different types (cf. mono and di-hybrids) are produced in equal

proportions. By random mating between these gametes all possible types of gametic combinations are obtained in the expected Mendelian ratios. Even in the cases where linkage is observed the gametes unite at random and there is no selective union. Therefore the deviation from the normal ratio must arise due to inequality in the number of different types of gametes. This *gametic proportion* in the hybrid can be tested in two ways (1) from F_2 data (2) by back-crossing. The second method is more widely adopted, and we shall first discuss the same here.

The double recessive parent always produces one type of gamete only, while the gametes produced by the hybrid are different and are in certain proportions. By back-crossing with the recessive which always produced one type of gamete only with recessive factors and consequently has no effect on the phenotype, the progeny obtained represents only the different types of gametes from the hybrid. Taking the progenies from the back-cross as 100 in the example considered in the preceding section, the following is a factorial representation of the data :

TABLE 19.

	With linkage.		Normal (without linkage).	
Hybrid (F_1)	*Stbf stbf Aa*		*Stbf stbf Aa*	
Gametes of F_1	*Stbf A* ...	10	*Stbf A* ...	25
	Stbf a ...	40	*Stbf a* ...	25
	stbf A ...	40	*stbf A* ...	25
	stbf a ...	10	*stbf a* ...	25
Gametes of B.C. male parent ...	all *stbf a*		all *stbf a*	
Back-cross progeny	*Stbf A stbf a* ...	10	*Stbf A stbf a* ...	25
	Stbf a stbf a ...	40	*Stbf a stbf a* ...	25
	stbf A stbf a ...	40	*stbf A stbf a* ...	25
	stbf a stbf a ...	10	*stbf a stbf a* ...	25
Proportion in B.C. phenotype:				
Fully feathered awnless ...	*Stbf A stbf a* ...	10	....	25
Fully feathered awned ...	*Stbf a stbf a* ...	40	....	25
Basal feathered awnless ...	*stbf A stbf a* ...	40	....	25
Basal feathered awned ...	*stbf a stbf a* ...	10	....	25

Actual back cross results show that out of 100 back-cross progenies, 40 in each of the parental types, and 10 in each of the recombined types appear. Where there is no linkage the four phenotypes appear in equal proportions *i.e.*, out of 100 total back-cross population, 25 in each appear. Therefore, it is evident that when the back-cross progenies are classified, the proportion in which the different gametes were formed by the hybrid is easily calculated. The total percentage of recombined types indicates the percentage of cross-overs. The percentage of cross-over is a measure of linkage and it is inversely proportional to linkage.

4. **Crossing over.**—This phenomenon was already discussed in Chapters V and VI. In genetic tests it is found that even in respect of the factors located

on homologous chromosomes, there are new combinations but these are generally fewer than the recombinations in respect of factors on different chromosomes. These genetical results have been corroborated by cytological observations.

Jannsens (1909) suggested that the paired chromosomes at meiosis break and rejoin and that chiasmata are the result of this crossing-over. This is termed *chiasmatype* theory and based on this, Morgan explained linkage. If *ABCDEF* and *abcdef* are two sets of genes arranged in this serial order on two homologous chromosomes, breakage and recombination between D and E will result in *ABCDEef* and *abcdEF* as resultant chromosomes.

It may be pointed out here that during prophase of mitosis the two chromatids are held together along their length ; in the prophase of meiosis the chromosomes are in single threads and the homologues come together. *Therefore it is suggested that the same force which holds the two chromatids together in mitosis, holds the homologues together at early pachytene.* Therefore at pachytene when the chromosomes are longitudinally split, the attraction between the homologues ceases and is replaced by the attraction between the two chromatids of the same chromosome. Since this attraction between the two homologues has ceased, the repelling force of the centromeres moves the homologues apart ; but these homologues have coiled round one another due to torsion and the chromatids have exchanged segments and they are criss-crossed.

Chiasmata are explained on two possible lines : (1) the chromatids break as a result of chiasmata and the breakage is after the formation of chiasmata. According to this, one of the paternal chromatids pairs with one of the maternal chromatids, (2) the chromatids have broken and rejoined at pachytene and as a result of this cross-over, chiasmata appear later. Therefore on either side of the chiasmata, sister chromatids of the same chromosome remain paired. This second hypothesis only is accepted and various evidences have been adduced for the same. At two strand stage of the pachytene, the bivalent chromosomes are spirally twisted round one another, and at the four strand stage they begin to move apart.

The position of chiasmata is at random and it never remains constant. The number of chiasmata in a bivalent may vary from 1.0 to as many as eight. The chiasma-frequency of any one region of the chromosome is generally the same as for any other region : *i.e.*, the chiasma is not generally localised. However, in certain organisms, chiasmata are restricted to particular regions of the chromosomes. For example, in *Fritillaria*, chiasmata are generally restricted to regions near to centromere. In such cases, the genes at farther ends from centromere do not cross-over and are therefore completely linked.

Formation of one chiasma means that there are 50% cross-overs. It is taken that a bivalent with 1.0 chiasma-frequency will be 50 'genetic units' long. On the basis of chiasma—frequency, genetic length of the chromosomes in various organisms have been calculated.

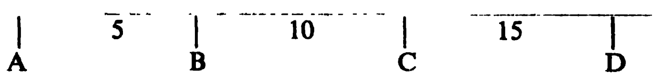
Normally, *cross-over at a particular locus, reduces the chances of another cross-over in its immediate neighbourhood.* There must be certain minimum distance between successive chiasmata. This phenomenon is termed *inter-*

ference. At a certain distance from the first chiasma, the interference disappears and a second chiasma may be formed. The phenomenon of interference can be studied both by genetical as well as cytological observations. The mechanics of interference is explained by the fact that the first cross-over has relieved the torsion strain by breakage and reunion and therefore the torsion is absent for some distance from that spot.

The percentage of crossing-over is not a constant feature but is variable under different environmental conditions. The environmental conditions under which gametes are formed have large influence on the percentage of crossing-over. For example, temperature is one of the factors. Plough's (1917) experiment is illuminating in two ways (1) it brings out the effect of temperature on crossing-over (2) it indicates the stage in the formation of the gametes when cross-over takes place.

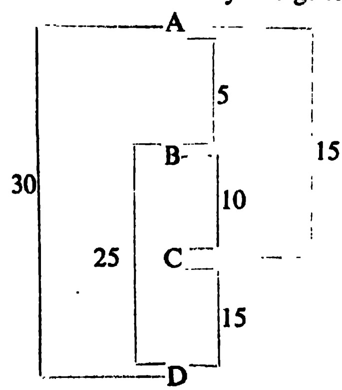
In *Drosophila* when the adult emerges from the pupa, about 150 eggs have been formed ; these mother cells are situated at the posterior end of ovarian tubules. The rest of the mother cells which are in front of them do not pass through meiosis at emergence. The adult at emergence was transferred to high temperature and therefore, the second set of mother cells underwent meiosis at higher temperature and consequently showed greater percentage of cross-over. This temperature does not alter the cross-overs in the first set of 150 eggs in the posterior end of the ovarian tubules. By another experiment, he showed that temperature changes *before* maturation division do not affect the cross-overs. Therefore, temperature has effect only when the homologous chromosomes are pairing during meiosis.

If cross-over values are interpreted as distances between the respective genes, it is found possible to predict the behaviour of new genes in relation to the already known ones. For example, if ABCD are linked together and their cross-over values are as shown in the figure below then the cross-over between one another of the series can be calculated.



A & B show cross-over value 5%
B & C show cross-over value 10%
The A & C show cross-over value 15%

Similarly the cross-over value between any two genes can be computed as shown below :—



This method of computing the distance between different genes is of limited significance due to the fact that there are many factors affecting cross-overs. The experiment must be conducted strictly under identical conditions of environments.

Sometimes, two genes may show apparent linkage due to *double cross-over*. By double cross-over the real distance between the genes is *apparently reduced*. In the preceding example, the calculated distance between A and C is 15 units. In actual tests, A and C may show apparent linkage due to double cross-over as shown below :—

ABC abc	No cross over
A-bc a-BC	Single cross-over between A and B
AB-c ab-C	Single cross-over between B and C
A-b-C a-B-c	Double cross-over with two breaks appearing simultaneously (vide fig. 43).

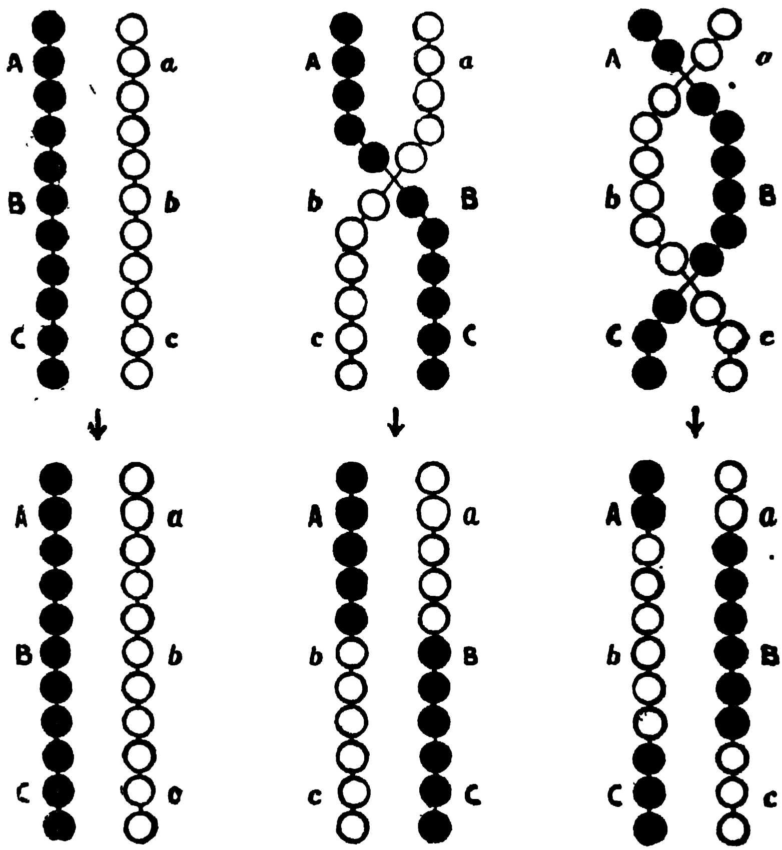


Fig. 43.—Crossing over (i) No cross over between A B C—a b c , (ii) Single cross over results in A b C —a B C . (iii) Double cross over results in apparent linkage between A. C,

It will be seen that in spite of two cross-overs the parental combinations A-C, a-c persist. By genetical tests one may be tempted to conclude that A and C are very close to each other ; in fact their actual distance is much greater and there is an apparent reduction in map distance due to double crossing over.

5. **Calculation of F_2 ratio.**—The F_2 ratio 9 : 3 : 3 : 1 or its modifications based on interaction of factors are applicable to cases where the factors assort themselves independently. In the cases where the factors are linked, the proportion in which the different genotypes occur in the gametes is altered.

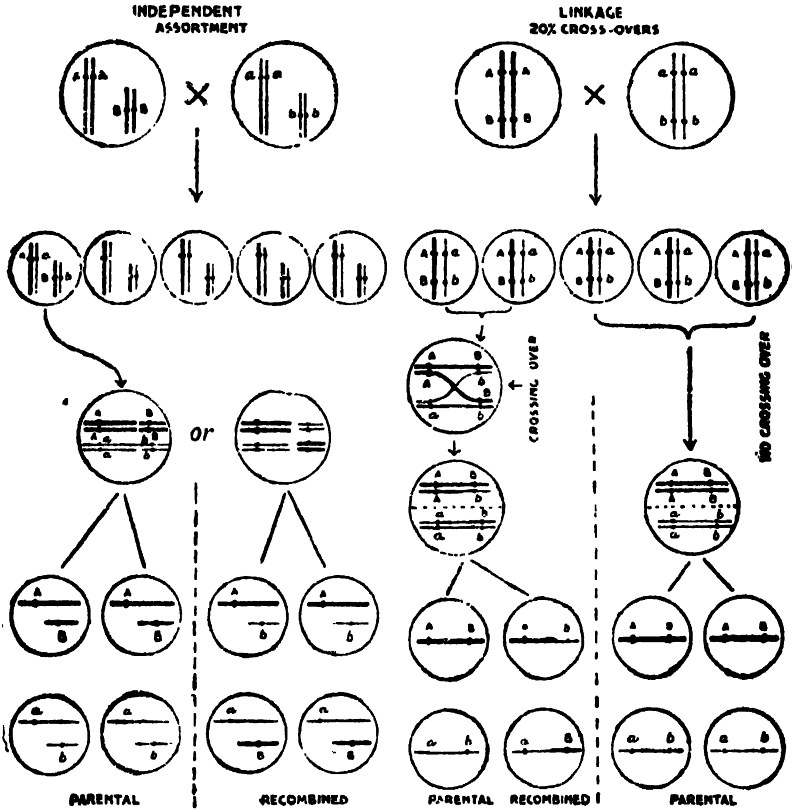


Fig. 44.—Diagram to explain independent assortment and linkage. When the factors A & B are located on different chromosomes, recombinations occur by the independent assortment of chromosomes. When A & B occur on the same chromosome, recombinations occur by crossing over. (The allelomorphs are distinguished by thick and thin lines). When there are 20% cross overs, 20% of gametes carry recombined chromosomes resulting from crossing over and 80% carry chromosomes as existent in the parents. In other words crossing over and exchange of segments take-place in two out of five mother cells during meiosis.

Consequently, on random mating, the frequencies in which the different genotypes occur in the F_2 population are also altered. If the cross-over value is known, the frequency of genotypes in F_2 can be calculated by taking into account the numerical proportion of the gametes in working out gametic combinations in the checker board. For instance in the example considered under Section 2, *Stbf* and *a* are linked yielding 20% of cross-over gametes

in F_1. It has been pointed out that in F_1 the parental types of gametes constitute 40% each and the recombined types 10% each (Fig. 44). When gametes of such proportion meet at random, the frequency of F_2 phenotypes can be easily calculated (Fig. 45).

F_1 gametes :	Stbf a 40% or 4	Stbf A 10% or 1	stbf A 40% or 4	stbf 10% or 1

When the gametes unite at random, the possible F_2 combinations are shown in checker board below :—

FIG. 45. CHECKER BOARD.

	Stbf a 4	*Stbf A* 1	*stbf A* 4	*stbf a* 1
Stbf a 4	16 awned fully feathered.	4 awnless fully feathered.	16 awnless fully feathered.	4 awned fully feathered.
Stbf A 1	4 awnless fully feathered.	1 awnless fully feathered.	4 awnless fully feathered.	1 awnless fully feathered.
Stbf A 4	16 awnless fully feathered.	4 awnless fully feathered.	15 awnless basal feathered.	4 awnless basal feathered.
Stbf a 1	4 awned fully feathered.	1 awnless fully feathered.	4 awnless basal feathered.	1 awnless basal feathered.

Fully feathered awnless	... 51	*Stbf A*
Basal feathered awnless	... 24	*stbf A*
Fully feathered awned ...	... 24	*Stbf a*
Basal feathered awned ...	... 1	*stbf a*
	100	

Conversely if the F_2 frequencies are known from the percentage of various phenotypes the value of linkage can be calculated by reference to standard tables.

6. **Linkage intensities.**—Many different methods are available for calculation of linkage intensities from F_2. When applied to the same set of data the different methods may yield different values for linkage intensity. Bateson and Punnett (1911) were the first to work out a method for calculating linkage intensity. Any method to be of wide applicability by breeders must be easy of calculation, statistically efficient and also the final values should not be seriously affected by field mortality of a few plants of any group. In this book, the method of Immer (1930) is given.

If p represents the cross-over percentage in repulsion phase, its value varies from 0 to 50% or 0 to 0.5 when expressed as a decimal fraction. In

coupling phase p represents parental combination and 1-p represents the cross-over percentage.

In F_2 segregation, if A and B are the factors involved, the four phenotypic classes will be of the type AB, Ab, aB, ab ; for briefness these four classes are designated as a, b, c, d, respectively. The method for calculating linkage intensities, as suggested by Immer and discussed here is known as *product method.* This is easy of calculation, and prepared tables are presented by the author so that many steps in calculation may be avoided by the breeder. This method is statistically efficient, since the magnitude of the probable error in this case is small.

It was already pointed out that linkage may be detected from F_2 data or from back-cross data. In statistical calculations, the bulk of the population, *viz.*, the number of plants from which the data are taken, is important to decide the ultimate reliability. The larger the population the greater the reliability. Given the same size of population, back-cross is more efficient than the F_2 data, since the probable error in the former is less than in the latter. It therefore follows that if F_2 population is taken for linkage study, the population size must be much larger than in back-cross. Further, the efficiency of F_2 data largely differs between coupling or repulsion phase of linkage. Thus for example, at 50% cross-over, the F_2 population must be 2.25 times back-cross population in coupling or repulsion phase. At 10% level of cross-over, 1000 individuals in back cross 1,130 individuals in F_2 coupling phase and 10,830 individuals in F_2 repulsion phase will give the same efficiency. Thus the F_2 data are not reliable for close linkage in repulsion phase.

Formulae for calculating the value of p from 9 : 7 and 3 : 1, 27 : 37 and 3 : 1, 15 : 1 and 3 : 1, 63 : 1 and 3 : 1, 3 : 1 and 3 : 1 are given by the author. The formula for linkage between two 3 : 1 ratios is :

$$\frac{ad}{bc} = \frac{2p^2 \times p^4}{1-2p^2 \times P^4}$$

For different values of p, the values of ad/bc have been provided in standard tables given by the author. In these tables ad/bc represents the products for repulsion and bc/ad for coupling. By direct reference to the tables the linkage values can be noted.

The following F_2 data may be considered as an example.

TABLE 20.

REPULSION PHASE.

(*a*) Stigma fully feathered awn nil.	(*b*) Stigma fully feathered awned.	(*c*) Stigma basal feathered awn nil.	(*d*) Stigma basal feathered awned.	Total N
206	75	76	2	359

$ad/bc = 206 \times 2/75 \times 76 = 0{\cdot}0723$

By reference to table 2 given by Immer, it may be seen that the cross-over value is roughly 18·00%.

Probable error for the same example is worked out by referring to the same table where the factor to be divided by $\sqrt{N}$ is given. At 18%, the factor is 0·6482. Therefore the probable error $= 0{\cdot}6482 \div \sqrt{359} = 0{\cdot}034$ or 3·4%.

Importance in breeding.—Linkage value between two genes is constant under given experimental conditions. Both environment and internal genetic constitution affect the linkage values. Work of Plough on *Drosophila* showed that temperature greatly affects the linkage values. The nature of effect of temperature appears to be of physical nature rather than chemical. It has been pointed out that cross-over at one point interferes with the same phenomenon on either side of that point. There are also specific genes which affect cross-over at certain blocks or regions of chromosomes.

For plant breeders, linkage is an important phenomenon. If any of the desirable characters of the crop plant are linked with any other undesirable character, cross-overs may not occur at all if the linkage is absolute. If the cross-over is low, then very few progenies may be of recombined form in the progenies of crosses. Linkage between characters is of very wide occurrence and this makes the plant breeder's problem difficult, because all possible recombinations in the progenies do not occur on account of linkage between the various characters in the parents entering the cross. In the case of cotton, two important economic characters are lint length and ginning percentage. In the case of American upland cottons, it is reported that naked seed and low ginning, fuzzy seed and high ginning are completely linked. Naked seed and high ginning will be most desirable but such a combination is difficult to obtain.

The phenomenon of linkage may be utilised to advantage by a plant breeder. It will be shown later that selection for quantitative characters in early stages of a cross, is beset with difficulties in truly judging the phenotypic values. If there is a qualitative gene which is linked with the genes responsible for quantitative characters, the former may be used as an index in selecting the progenies. Such an association may not be possible due to the fact that the genes for quantitative characters may be located in more than one chromosome in which case linkage between all of them and a qualitative gene is not possible. However, in cholam it was found that in a cross between Kafir and Milo sorghums, the factor Mu (wavy leaf blade) was always associated with big panicles, broad leaves and thick stems.

The following are a few other examples of close correlation between morphological and quantitative characters.

Cotton.—Corolla colour and lint index. Red plant body and length of vegetative period ; lint colour and lint length.

Rice.—Sterility and growing period ; Anthocyanin pigment and yield ; Anthocyanin pigment and tillering ; colour of grain and weight of grain.

If the correlation between the characters is due to genetic causes, *viz.*, that the genes are closely situated on the same chromosome, a breeder can hope to break the combinations under extraordinary conditions, such as x-raying etc., and get recombinations. If the character combinations are purely physiological and recombinations fail due to physiological incompatibility, the breeder cannot secure recombinations. In *G. arboreum*, there are types which are high ginners but with poor lint qualities ; there are other types which are low ginners but with fine lint qualities. Attempts by cotton breeders to combine high ginning and fine lint quality by hybridising the two types have so far failed. The negative correlation between these two desirable characters may prove to be due to genetic causes, but the problem remains so far unsolved. In rice, height of plant is correlated with duration and this limits the possibilities of securing tall growing short duration types. Under South Indian conditions, duration and yield are correlated and the possibilities of securing high yielders of very short duration are remote. From other experiments it is concluded that the correlation here is on physiological basis. Similarly, packed arrangement of panicle and big size of grains could not be combined in paddy.

There are various other examples, where the plant breeders have met with limitations to their ambition due to close linkage between the characters. The work of Anderson (1939) on the cross between *Nicotiana alata* and *N. Langsdorffii* showed that linkage of multiple factor characters is high. In addition to the restrictions due to linkage, other phenomena such as gametic elimination, zygotic elimination, and pleiotropism also restrict recombinations appearing freely in F_2 generation of a cross. Recombination is generally restricted to a fraction of the total—less than 1/64. They are restricted to types which are more or less like the two parents and the hybrid. There is no free shuffling of parental characters in F_2 generation. This is further discussed in chapter XIX.

8. **Sex linked characters.**—In the case of plants such as cholam, rice, etc. both the sexes occur in the same plant. There are a few dioecious plants such as date palm, palmyrah, hemp etc., where the sexes are in separate plants. The mode of sex inheritance in these cases is not clearly understood. The chromosomal mechanism in relation to sex determination was already dealt with in chapter VII. XY, XO and WZ types of chromosomal mechanism have been explained there. If genes are situated on chromosomes and if particular combinations of chromosomes cause the development of one sex or another, it follows that all factors on sex chromosomes will show one type or other linkage with sex. A large number of such instances have been met with where certain characters went with one sex and the character is then described as *sex-linked.* Sometimes sex-chromosomes are termed as heterosomes in contrast to autosomes and therefore the factors on heterosomes are referred to as *heterosomal factors*, and the sex linked inheritance is referred to *heterosomal inheritance*. Therefore sex linked factors are situated on sex-chromosomes. There are instances where, though the factor is situated on autosomes, the character appears in one sex only, or the factor varies in its expression in the two sexes. Secondary sexual characters are examples for this.

In fowls, when ovary is removed from hens, they develop male characters. Here, the females are heterogametic and in early stages of development, the sex chromosomes bring about certain effects, probably by the production of hormones, which inhibit the development of characteristics of the opposite sex. Sex-limited characters need not always be characters pertaining to sex. For example in Ayrshire cattle, the mahogany colour (M) or red colour (m) is found in homozygous state in both the sexes. But when heterozygous, males are mahogany and females red. Therefore the expression of the factor Mm varies with the sex, though in homozygous form MM, or mm, its expression is not affected by sex.

In Dorset breed, which is horned in both the sexes the development of horn shows distinct difference in the two sexes. Suffolk breed is hornless in both the sexes. A cross between the two breeds, shows the following interesting results.

Parents : Hornless ♀ × Horned ♂

↓

F_1 : Hornless

Horned

F_2 : ♀♀ = 3 Hornless : 1 Horned

♂♂ = 1 Hornless : 3 Horned

In the Reciprocal cross :

Parents : Horned ♀ × Hornless ♂

↓

F_1 : Hornless ♀♀

Horned ♂♂

F_2 : ♀♀ = 3 Hornless : 1 Horned

♂♂ = 1 Hornless : 3 Horned

This is explained by the assumption that the horned condition is dominant in male and recessive in female.

The sex-limited characters need not therefore be always characters relating to sex. The sex chromosomes affect the expression of these characters.

Factors which are located on sex chromosomes are sex-linked in inheritance. Red Vs. White eye colours in *Drosophila* form an allelomorphic pair with red as dominant.

The results of the cross vary according to the eye colours of the female and male entering the cross.

Parents : Red ♀ × white ♂

↓

F_1 : Red ♀♀

Red ♂♂

F_2 : 2 Red ♀♀ : 1 Red ♂ : 1 white ♂

In the reciprocal cross

Parents : white ♀ × Red ♂

↓

F_1 : Red ♀♀

white ♂♂

F_2 : Red ♀ : 1 white ♂

1 Red ♂ : white ♂

In the first cross the hybrid and F_2 females are always red. In the second cross, the character is reversed in the two sexes in the hybrid and this is termed as *criss-cross* inheritance. The sex-linkage in this experiment may be explained as follows.

The factors for eye colour are borne by X-chromosomes and Y-chromosome has no effect on eye-colour development.

The phenomenon of sex linkage is in no way different from linkage in respect of other characters. Over 100 sex linked characters which have been studied in *Drosophila melanogaster* affect every part of the body such as eye colour, body colour etc. The chromosomes XX, XY or WZ, ZZ only act as differential in determining sex ; otherwise they may bear other factors and conversely many factors affecting sex are located on autosomes.

In explaining the eye colour of *Drosophila* it was assumed that the Y chromosome does not carry any factor for eye colour. It is found by extensive experiments that only one factor - 'bobbed' - is located on y chromosome. Large portion of the y-chromosome is 'inert' without genes. Similar is the behaviour of W chromosome. The W and Y chromosomes are sometimes referred to as *allosomes.*

9. **Linkage values in some crop plants.**—The data for linkage values in crop plants is meagre and scattered. No attempt is made here to bring together such data, but a few examples are given here to familiarise the reader with such information.

Crop.	Phenotype.	*% cross over.*
Cholam ...	Nucellar layer in grain and glume colour	25
	Nucellar layer in grain and green stripe in plants	12

Crop.	Phenotype.	% cross over.
Cholam ...	Nucellar layer in grain and glume colour.	16
	Brown wash on grain and sheath-cum-glume colour	16
	Leaf tip hairiness and stigma basal feathered	25.0
	Awn nil and stigma feathers basal ...	18.0
	Red coleoptile and mid rib colour ...	21.5
	Seedling stem colour and juiciness of stalk.	10.9
	White seedlings and red coleoptile ...	41.34
	Plant colour purple and juiciness of stalk.	30.0
	Plant colour purple and seedling stem colour	16.4
	Plant colour purple and coleoptile purple	18.0
	Crustaceous glume and juiciness of stalk ...	17.0
	Yellow seedlings and waxy endosperm ...	26.5
	Eligulate leaves and axillary shoots in panicle	0.01
	Yellow leaves and stems and pericarp colour	13.0
	Pale green seedlings and zygotic lethal ...	23.5
Maize ...	Complementary factor for colour and non-waxy endosperm	21.7
	Complementary factor for colour and shrunken endosperm	2.3 (*f*) 3.4 (*m*)
	Complementary factor for colour and polkadot leaves	2.0
	Complementary factor for colour and variegation	30.0
	Polkadot leaves and shrunken endosperm.	10—16.4
	Shrunken endosperm and white seedlings.	22.3
	Virescent seedlings and waxy endosperm ...	7·0
	Dwarf and shrunken endosperm ...	22·9
	Virescent seedlings and shrunken endosperm	20·0
	Virescent seedlings and waxy endosperm ...	19·0
	Male sterile and shrunken endosperm ...	22·2
	A complementary factor for colour of aleurone and golden plant	23·0
	A complementary factor for colour of aleurone and yellow seedlings	1·6

Crop.	Phenotype.	% cross over.
Maize ...	Yellow seedlings and golden plant ...	19·0
	A complementary factor for colour of aleurone and yellow seedlings	33·9—35·4
	A complementary factor for colour of aleurone and pale green seedlings ...	23·3
	Pale green seedlings and lineate leaf ...	44·6
	A complementary factor for colour of aleurone and white seedlings. ...	17·0
	Lineate leaf and white seedlings ...	22·0
	A complementary factor for colour of aleurone and virescent seedlings ...	20.0
	Sugary endosperm and tunicate ear ...	28.6—29.6
	Sugary endosperm and virescent seedlings.	32.4
	Sugary endosperm and white seedlings ...	20—22
	Intensifier of plant colour and liguleless leaf	30.32
	Intensifier of plant colour and silkless ...	10.5
	Intensifier of plant colour and virescent seedlings	16.8
	Liguleless leaf and virescent seedlings ...	43.2
	Yellow endosperm and purple plant colour	29·7
	Yellow endosperm and yellowish leaf ...	33·0
	Yellow endosperm and white seedlings ...	35.0—42.0
	Yellow endosperm and male steriles ...	4.2
	Tassel seed and pericarp colour ...	1.0
	Pericarp colour and fine striped leaf ...	35.0
	Pericarp colour and brachytic culms ...	35.5 38.0
	Adherent tassel and brachytic culms ...	16.8 30.0
	Ramosa ear and brown aleurone ...	38.2
	Brown aleurone and glossy seedlings ...	18.7 29.4
	Brown aleurone and irrescent seedlings ...	24.9
	Glossy seedlings and virescent seedlings ...	6.2
	Brown aleurone and pale green seedlings ...	4.5
	Vivipary in maize and purple aleurone ...	30.0
	Purple aleurone and brevis dwarf ...	21.7

Crop.	Phenotype.	% cross over
Maize ...	Brevis dwarf and virescent seedlings ...	23.0
	Crinkly leaf and male steriles ...	30.0
	Non-reduced endosperm and vivipary	15.5—1.21
	Ragged and defective endosperm ...	11.9
	Tassel seed and rugged	1.7
	Pale green seedlings and defective endosperm	32.0
	Crinkly leaf and defective endosperm ...	18.0
Rice ...	Tawny colour in glume apices and awns-and-non-glutinous rice	16.59
	Colourless apiculus and non-glutinous rice	22.34
	Leaf sheath colourless and non-glutinous rice	19.43
	Length of outer glume and short spikelet.	1.11
	Stigma colour and leaf sheath colour ...	9.8

Chapter 8

VARIATION

VARIATION—ACQUIRED CHARACTERS—VARIATIONS DUE TO ENVIRONMENT—AUTOGENOUS VARIATIONS—GRAFT HYBRIDS AND CHIMERAS—PARALLEL VARIATION—GENERAL.

1. Variation.—Bateson (1906) in defining the term genetics which he coined then said " *it deals with physiology of heredity and variation.*" " *It is a science which seeks to account for the resemblances and differences exhibited among organisms related by descent.*" While heredity deals with " *the genetic continuity of germinal material between parents and offspring, variation accounts for the differences between organisms related by descent.*" The differences between organisms related by descent are of two kinds (1) *the differences may be due to those present in the gametes which gave rise to the organism* (2) *the differences may be due to differences in the expression of somatic characters due to environment.*

No two individuals are identical in all respects. Each individual is unique in itself. All features of an organism, morphological or physiological are subject to variations of two types pointed out above. The environment, such as soil conditions, atmospheric temperature, humidity, etc., are never strictly identical for any two individuals. Due to this difference in the environment the expression of the genotype is variable. This variation which is caused by differences in the environment is termed *developmental variation* or *fluctuating variation.* Since this variation is caused by environment, it is never inherited by the progenies. Taking for example, a crop plant like rice, which is cultivated since some thousands of years in different countries like India, Japan, China, Africa, Italy, Spain, etc., and has gone through varying seasonal and soil conditions the plant has preserved its characteristics and taxonomically all the varieties fall into one species—*Oryza sativa.* A vigorous growing variety of Japan when raised under South Indian conditions may become stunted. Whereas, genetically controlled characters like glume colour, number of florets in a spikelet will not be altered. A variety of rice which grows vigorously in a well manured and fertile soil, may be stunted when raised in poor soil. The essential features of a rice plant, which distinguish the same from any other species are not altered by the variations due to environment.

The type of variation which arises due to differences in the genetic make up of the gametes are hereditary. An improved rice strain like G. E. B. 24 which is but a multiplication from a single plant selected about the year 1922, is still showing the characteristics which distinguished its ancestor from the rest of the varieties. Though the variety has been under cultivation for the last two decades and more under different soil and climatic conditions it has not lost its primary characteristics.

Though variation is the rule in Nature, it falls under the two categories pointed out above ; *viz* : (1) variations due to environment and which are

not hereditary (2) variations due to genes and which are hereditary—autogenous variations. *The first type of variation is of immediate consequence to the individual, while the latter is of importance to the progenies and in evolution.* Variation may arise in the course of development of the individual (*ontogeny*) or in the course of its ancestry (*phylogeny*). From what has been stated above it is evident that developmental or fluctuating variation has no part to play in evolution or phylogeny : the variation which arises in ontogeny may fall into the two groups mentioned above *viz.*, developmental or genetic. Earlier biologists did not distinguish between these two types of variations, because they were labouring under blending of characters in inheritance, and the particulate inheritance was proved beyond doubt in 1900 only by the rediscovery of Mendel's publications. Prior to this period, the variations arising in the course of ontogeny were termed acquired characters and much confusion prevailed as to its role in evolution.

2. Acquired characters.—It is now known that the characters of an individual may vary due to (1) environment or (2) genetic causes. Such a distinction was not clearly realised when theories on evolution were enunciated in the eighteenth and nineteenth centuries. Some stated that acquired characters were inherited and others held that they were not. It is of utmost significance for a plant breeder to know whether acquired characters which are induced by environmental conditions are inherited. If so, seeds harvested from fertile plots which receive heavy dose of manure, optimum irrigation and favourable climatic conditions may yield equally well in any other field in the succeeding seasons without such optimum environment. The importance of acquired variation first received the attention of Lamarck (1744—1829) who considered that the variations induced in the individual as a result of interaction with the environment are of significance in evolution. *According to Lamarckism all variations are acquired and all variations are heritable.*

The same problem was later considered by Darwin (1859) in his book on " Origin of species." Charles Darwin was a naturalist with keen observations. He considered that some of the acquired characters are heritable and that other variations are of spontaneous origin. These two variations constituted the adaptability of the organism to the environment. Darwin's theory of organic evolution is further discussed in detail in chapter XII.

Weismann (1834-1914) who conducted experiments by artificially inducing variations by mutilation etc., concluded that acquired characters are not inherited. He developed the *germ plasm theory* according to which the germ cells and body cells are separate and distinct, being constituted by germplasm and somatoplasm respectively. Many later experiments confirmed Weismann's conception that acquired characters are not inherited even though his germplasm theory is not valid.

One of the recent experiments that illustrates the point was performed by Castle and Phillips on guinea pigs. The ovary of a black guinea pig was operated and transplanted into a white guinea pig. After nearly a year, the operated white guinea pig was mated to another white male. The progeny was black showing that the ovary from the black animal has not changed.

Bonnier planted in the alpine regions a few species of plants from the plains. These species changed in their morphological appearances due to the effects of new environment. In some instances the change effected was so much that it almost resembled another species on the plains. This is termed "*new place effect*". After 18 years of acclimatisation in the alpine regions when the plants were returned back to their original habitat on the plains they reverted back to their original characteristics, showing that the environment did not alter the breeding behaviour.

Now there are overwhelming evidences to show that the effect of external environment on the development of characters is not hereditary ; but any change in the genotype which may arise due to environment may be inherited. For example, x-ray induces new changes in characteristics which are heritable ; these genotypic changes which arise in the course of ontogeny are termed *mutation*. Mutation may involve a single gene, part of a chromosome, a single chromosome or a whole haploid set of chromosomes. Mutation may take place in somatic or germ cells and this type of acquired genotypic change is discussed in chapter IX.

3. **Variations due to environment.**—From the preceding section it is evident that variations may arise due to external causes—*exogenous*—or due to internal causes—*autogenous*. *Favourable environment is necessary for the genotype to develop the characters.* For example, the development of chlorophyll pigment on plants is controlled both genotypically and by environment. Absence of manganese iron, light or magnesium may lead to chlorophyll deficiency. One or more genetic factors may also control chlorophyll development. In Sorghum two factors C_1 and C_2 are responsible for developing shades of greenness in different varieties.

Yield and quality of crops are complex characters and are governed by various attributes. They are governed by a large number of genetic factors. These characters are largely influenced by environment also.

In table 21 yields of 5 cotton strains tried in 12 different centres are presented. The yield data reveal that none of the strains are cosmopolitan in their behaviour. Their responses to the varying environmental conditions in the 12 centres are not uniform. The data further show that even though yield is a genetically controlled character it is largely fluctuating with environment.

That these differences in yields are not due to variability or impurity of the seed material used in the different centres is concluded from another experiment. Ten sibs from each one of the strains were tried in compact family block for yield and the data are shown in table 22.

Except in the case of Co_3 there is no difference among the sibs. In respect of the other four strains, yield differences are due to environment.

Soil, water, temperature and light are some of the chief factors in environment.

TABLE 21.

DISTRICT TRIALS IN RESPECT OF 5 STRAINS OF AMERICAN COTTON IN THE MADRAS PRESIDENCY, 1941-'42.

PLACES OF TRIAL.	Names of improved types, Yield of Kapas in lbs. per acre.					Names of improved types : Yield expressed as percentage over Co.2 as control.					Conclusions.
	Co2	920	Co3	Co4	4463	Co2	920	Co3	Co4	4463	
	(1)	(2)	(3)	(4)	(5)	(1)	(2)	(3)	(4)	(5)	
Coimbatore District—											
1. Suripalayam ...	1,099	1,111	685	780	829	100	101	62	71	75	2·1·5·4·3.
2. Nanjagoundenpalem ...	1,406	1,550	1,010	1,383	1,410	100	110	72	98	100	2·5·1·4·3.
3. Poondurai ...	450	488	454	277	361	100	108	101	62	80	2·3;1·5·4.
4. Pongalur	1,173	1,139	803	764	968	100	97	68	65	83	1·2·5·3·4.
5. Muthannapalem ...	1,406	1,483	1.375	1,351	1,430	100	105	98	96	102	'Z' test not satisfied.
6. Akilandapuram ...	1,400	1,367	938	1,336	1,226	100	98	66	95	88	1·2·4·5·3.
7. Pedappampatti ...	203	152	155	211	206	100	75	76	104	101	4·5·1·3·2.
8. Chinnakomarapalem ...	959	849	951	625	877	100	89	99	65	91	1·3·5·2·4.
Trichinopoly District—											
9. Kuppuchipalem ...	1,183	1,100	1.218	1,213	1,131	100	93	103	102	96	'Z' test not satisfied.
10. Vaiyampatte ...	891	956	1,102	1.125	1,128	100	107	124	126	127	
Madura District—											
11. Lakshmipuram ...	974	1,073	925	951	955	100	110	95	98	98	
12. Reddiarchatram ...	1,498	1,607	808	999	1,116	100	107	54	67	74	

(*Data from Madras Agriculture Station Reports* 1941—'42.)

Soil.—Every agriculturist knows that his success largely depends upon the fertility or otherwise of his soil. Since the plants depend upon the soil for minerals, any deficiency in the soil is reflected during development. In poor soils, the plants are stunted and in rich soils they are vigorous. Deficiency in essential elements may cause deficiency diseases, *e.g.*, deficiency in iron or magnesium may cause chlorosis. Soil condition may also influence flowering duration. Poor vegetative growth may force the plant to flower earlier and rank vegetative growth may delay flowering. In some cases, seeds

TABLE 22

Variability among Sibs

YIELD OF KAPAS IN ¼ OZ. PER PLOT.

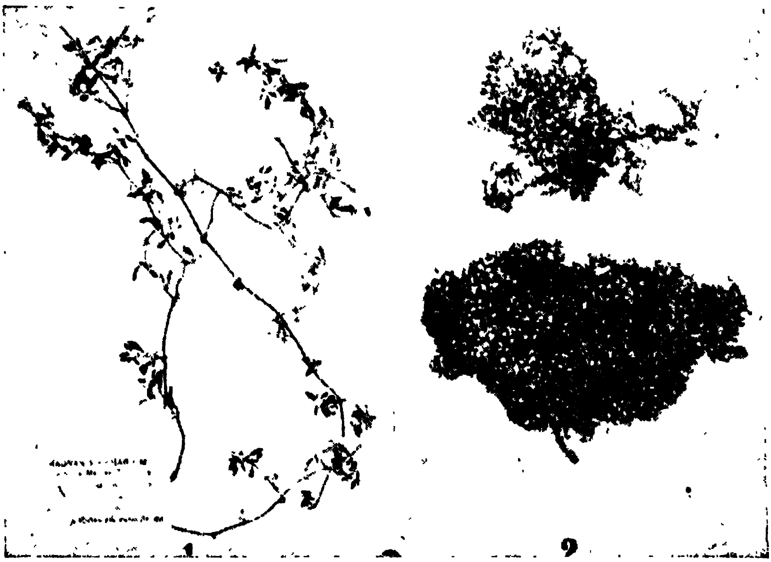
SIB No.	Co.2.	920.	Co.3.	Co.4.	4463.
1	24·08	28·74	23·03	26·34	27·42
2	33·22	34·59	28·22	32·24	36·09
3	33·14	35·79	26·28	29·74	26·87
4	29·48	37·49	34·73	32·94	35·40
5	30·75	34·39	30·13	26·09	31·02
6	39·70	36·57	32·32	33·14	35·94
7	33·89	43·47	26·33	27·14	26·49
8	32·83	37·07	26·38	29·19	35·62
9	36·17	35·49	26·77	33·04	35·90
10	26·75	34·90	25·68	24·69	28·90
Mean ...	32·90	35·85	27·99	29·54	31·97
Significance ...	No.	No.	Yes.	No.	No.
C.D. for Co.3—5·1					

secured from well manured and fertile soils yield better for one or two seasons as compared to seeds from poor soils. Seed multiplication in Russia is carried out in fertile soils as such seeds produce vigorous progenies due to initial advantages in the reserve food materials in the seed.

Soil condition determines the nutrition in the plants. Nutrition in general has a large influence over developmental variations.

Water.—Plant growth is highly correlated with water relations of soil and conditions of moisture during the growth period. Any change in the optimum conditions will affect normal development. In nature, plants are adapted to their natural habitat. Thus xerophytes may develop thick cuticle, dense hairiness, well developed vascular systems, thorns or prickles, waxy bloom, thick leaves with water storage tissues or reduced leaf surface. When plants which have developed these adaptations are raised under conditions with excess of moisture, these modified anatomical or morphological structures

may become reduced or completely suppressed. Thus, *Opuntia dillenii* when raised in water cultures may not develop the thorns. Hydrophytes also show similar behaviour. *Hygrophylla heterophylla* develops one type of leaf under water and another type above the level of submersion. Fig. 46 shows *Alternanthera paronichioides* and the change in habit has been caused by water relations in the habitat.



(*Specimens collected by Daniel Sundar Raj.*)

Fig. 45.—Variation due to environment. *Alternanthera paronichioides*. On the left is a plant growing near water channels and on the right is a plant growing in dry regions.

Moisture in the surrounding atmosphere, *viz.*, humidity of the atmosphere, has also influence on the variations in the plant. High temperature in combination with humid atmosphere is responsible for dense tropical forests. Atmospheric humidity has great influence not only on the final yield but also on the quality of the produce. Continuous moist weather and want of proper conditions for ripening as in Taliparamba in the West Coast of Madras are not conducive to sugarcane growing. Fibre development in the cotton boll is conditioned by the atmospheric humidity.

Temperature.—This is one of the factors having great influence over the developmental variations. The development of white or red flower in *Primula* is largely affected by temperature. The crop plants in their distribution and growing season are temperature bound. Thus, rice is a tropical crop requiring heat and humidity though there are varieties thriving in temperate zone also. With mean temperature below 75°F. it is not successfully raised. Total temperature required is computed to be between 2,500 and 4,000 in Spain and Italy. In Madras it varies from 7,500 to 16,800. There is great deal of varietal variation. In the case of *Drosophila* it was noted that the expression of " vestigeal wing ", a genotypically controlled character depends upon the temperature of the medium in which the larvae are reared.

By treating eggs of moths to particular temperatures at sensitive periods, Goldschmidt produced changes in the development of wing patterns in butter flies without altering the genotypes. These changed patterns exactly resembled certain mutants. Such developmental changes are termed *phenocopies.*

Light.—In the case of plants bearing chlorophyll, light is an essential factor. In the absence of light chlorophyll does not develop and elongation of cells is rapid causing etiolation. Some crop plants like tea and cardamomum require shade for their normal development while others like cholam, paddy, etc., come up in direct sunlight. When optimum sunlight is not available, the plants may become pale green and less vigorous. Such pale green appearances may also be due to genotype as pointed out in chapter VI, in which case, even under optimum conditions for development of chlorophyll, the plants will not attain dark green colour. Similarly, in pearl millet (*Pennisetum typhoides*) factor *E* was found responsible for efficient development of chlorophyll and in the absence of the factor the crop appears pale green. Albino seedlings were noted in a number of crop plants and these lack the genetic factors which are responsible for the development of chlorophyll. Therefore they appear white from the time of germination and when the reserve food in the seeds are exhausted, they die. All these point to the fact that when genotype does not limit the development of chlorophyll, light acts as the limiting factor.

In the case of leaf sheath colour in rice, the development of red anthocyan pigment, which is genotypically controlled develops only in portions exposed to light, while portions not exposed to light do not develop the pigment. But light is not essential in all cases of pigmentation. In the case of pigment development in the stigma of rice plants light is not essential. In cholam, light is an essential requirement for pigment development in the shoots while pigment development is complete in the roots even in the absence of light. In the case of purple mutant in cholam, purple colour develops even around the deep seated vascular bundles. Therefore it may be stated in general, the limiting action of light depends largely on the genotype.

Earliness in crops like rice and cholam is a Mendelian character but it is also governed by light, an important environmental factor. Garner and Allard have shown that the flowering-period of plants can be affected by *photo-periodism.* According to their reaction to photo-period, plants are classified as (i) long day plants (ii) short day plants (iii) plants indifferent to light period. This aspect is further dealt with in greater detail in Chapter XXI.

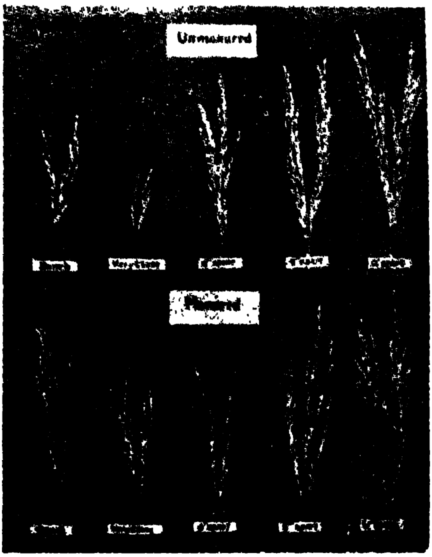
According to Lysenko, photo stage is the second phase in the phasic developments of plants in vernalisation. Here it is shown that light has very great influence on the developmental phases of the plant.

From the foregoing discussions on the effects of environment on development it is evident that, *for normal expression of genetic factors, environmental conditions must be favourable* ; *that in some instances, the appearances of individuals may be alike but yet in one case it may be due to environment while*

in the other it may be due to altogether a different genotype. Genes may express themselves phenotypically or not but in either case they have a bearing on the breeding behaviour of the plant.

The variations due to environment are important both to agriculturists and to plant breeders. The agricultural practices of a country are designed to bring about maximum variation in the desired characters and in desired directions. (Fig. 46.) The plant breeder aims at selecting genotypes that yield maximum benefit to the cultivator. In making this selection, it will be shown later that the developmental variations affect the proper evaluation of the genotype. Therefore, detailed knowledge regarding the influence of environmental factors on economically important characters is essential.

In the case of cotton, fibre is the economic product. Of the various fibre qualities, lint length, ginning percentage and maturity are the most important (Fig. 47). The former two are governed by a large number of genetic factors. Variation in these measurable characters have been recently studied and the results are summarised below so as to point out the type of developmental variations met with in quantitative characters even in pure lines.



(With the permission of Curr. Sc.)
Fig. 46.—Developmental variations in rice panicles.

Variations under the following conditions have been studied.

(1) Variation between regions of the seed surface.

(2) Variation between seeds in a lock.

(3) Variation between locks.

(4) Variation between bolls on a plant.

(5) Variation between weekly pickings.

(6) Variation between first and second flush of bolls.

(7) Variation due to irrigation.

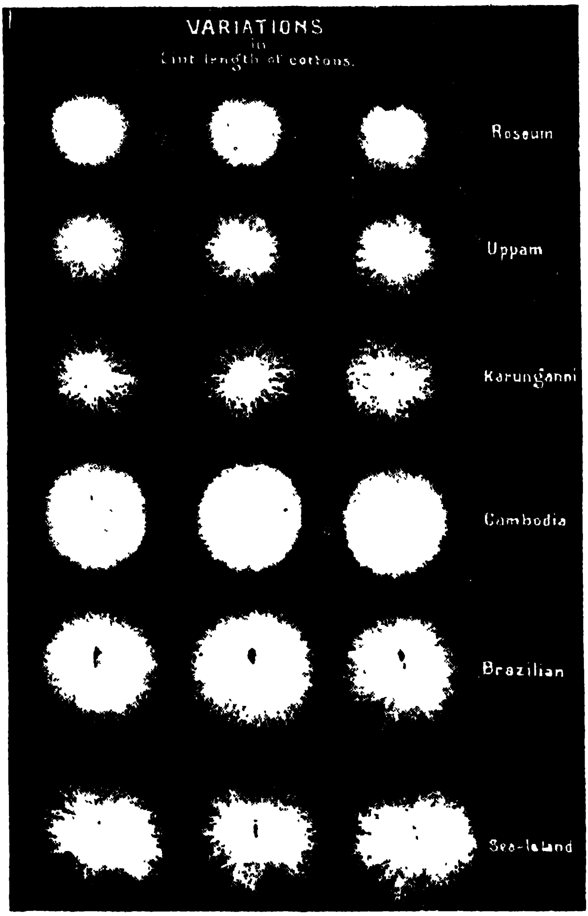
(8) Variation due to spacing.

(9) Variation due to rotation.

(10) Variation due to manurial treatment.

(11) Variation caused by change of place and season.

(1) *Variation between regions of the seed surface.*—Variability of the length of fibres in different regions of the seed has been assessed by coefficient of variation of the length distribution as estimated by Bolls sorter. The coefficient of variability ranged from 14.0 to 25.1 %. The variability was higher



(Photo from Cotton Specialist.)

Fig. 47. Halo length in cotton. The figure shows the variation in lint length and ginning percentage in the different types under cultivation.

as micropylar end. In the case of the cambodia pure line (Co. 2) tested, the mean value for the micropylar region was 0.85" and that for the chalazal region 1.00". Similarly, the mean fibre weight per c.m. at micropylar end was 2.88 while that for chalazal end was 1.44. The mean fibre maturity for

chalazal end of seed was 30.1% while that for micropylar end was 88.0. The standard fibre weight for chalazal end was 1.93 while that for micropylar end was 2.68. The fibre attachment to the seed is strongest at the micropylar end and weakest at chalazal end.

In brief it may be stated that (1) at the micropylar region the fibres are thinly populated, short, very mature, have the highest fibre weight, standard fibre weight, fibre diameter, fuzz diameter and fibre strength and are most firmly attached to the seed. (2) at the chalazal end the fibres are densely populated, are longer and more immature, have smaller weight per c.m., standard fibre weight, fibre diameter, and fibre strength and are less firmly attached to the seed and (3) at the other regions the variations among themselves do not appear to be conspicuous ; generally speaking the values lie intermediate between those for the two regions considered above, though they approach the values for either of the two regions in some cases. The probable cause for variations in the fibre properties in different regions of the same is differential nutrition.

(2) *Variation between seeds in a lock*.—The positions of the seed in a lock are serially numbered from the pedicel end.

Variation in respect of fibre properties are noticed among the seeds in a lock. In respect of two strains of cotton, Co. 2 (*G. Hirsutum*) and K. 546 (*G. arboreum*), the following variations have been noticed.

(*a*) The mean fibre length gradually rises from first to last in Co. 2 while in K. 546 it rises upto the middle of the lock and falls later on.

(*b*) The fibre weight per c.m. does not indicate any variation in Co. 2 while in K. 546 there is a consistent fall from first to last position.

(*c*) Unit fibre weight shows no variation in Co. 2 but exhibits a gradual fall in K. 546.

(*d*) The number of fibres per seed as well as the number per unit area gradually decreases towards the end of the lock.

(3) *Variation between locks*.—As regards variations between locks, it may be summarised that, generally seed weight, lint weight and embryo weight appear to increase with the decrease in the number of seeds in the lock.

(4) *Variation between Bolls in a plant*.—There are contradicting observations in respect of variations between bolls in a plant. There are distinct differences between bolls on a plant. Bolls in the lower half of the plant which are generally the earlier formed ones, give shorter length (Kearney & Harrison). While some investigators found variation along the vertical and horizontal axes, others found none. The apparent contradictions are due to differences in the materials tested, culture, climate, maturation period, age of plant, etc.

(5) *Variation between weekly pickings*.—Seed weight, lint weight, mean fibre length, number of convolutions per unit length, number of fibres per seed

TABLE 23.

VARIATION BETWEEN WEEKLY PICKINGS.

Weekly Pickings.	Seed Weight.							Lint Weight.							Ginning Percentage.						
	2405.	H1.	N14.	171.	C-7 —CBE.	C-7 KPT.	Co-2.	2405.	H1.	N14.	171.	C-7 —CBE.	C-7 KPT.	Co.2.	2405.	H1.	N14.	171.	C-7 —CBE.	C-7 KPT.	Co.2.
I ...	79	71	51	55	52	56	140	26	28	16	20	26	28	76	25	29	24	26	34	34	35
II ...	72	72	53	53	51	56	146	26	29	26	18	26	27	80	26	29	23	26	34	33	35
III ...	72	73	52	55	49	55	147	26	33	15	18	24	27	76	26	31	23	25	33	33	34
IV ...	65	73	51	56	48	51	140	24	33	15	18	24	26	74	27	31	23	24	33	34	34
V ...	64	67	51	55	48	50	137	24	31	16	16	21	26	74	27	32	24	32	31	34	35
VI ...	58	64	49	56	48	50	133	20	29	16	16	21	24	70	26	31	24	22	30	32	34
VII ...	58	60	46	...	48	48	131	22	25	14	...	21	22	68	27	30	24	...	30	32	34
VIII ...	55	55	45	...	50	48	126	20	25	13	...	23	22	63	27	32	23	...	31	31	34
IX ...	53	...	...	...	...	44	...	20	...	...	...	...	18	...	28	...	...	...	...	29	...
X ...	53	...	...	...	...	...	...	20	...	...	...	...	...	...	27	...	...	...	...	...	...
	Mean length in inches.							Number of fibres per seed in 000's.							Immature fibres—%.						
I ...	·97	·95	·94	·88	·89	·86	1·03	4·83	5·62	3·36	4·44	5·69	6·78	15·2	2	2	2	3	16	6	20
II ...	·93	·99	·93	·85	·87	·91	1·04	4·75	5·82	3·23	4·30	5·57	6·25	16·2	3	3	1	3	16	8	17
III ...	·92	·93	·94	·82	·86	·88	1·03	4·48	6·12	3·39	4·08	5·62	6·27	15·6	3	2	2	3	20	6	22
IV ...	·87	·95	·93	·83	·88	·86	1·03	4·43	6·16	3·34	4·13	4·25	6·00	15·1	3	2	2	2	17	5	22
V ...	·86	·89	·98	·86	·86	·89	1·03	4·65	6·35	3·38	3·86	5·22	5·90	15·7	3	2	2	3	17	3	25
VI ...	...	·86	·92	·87	·89	·90	1·01	...	6·29	3·38	3·70	4·83	5·52	15·4	...	2	2	4	16	11	25
VII ...	·78	·81	·88	...	·92	·88	·95	4·35	6·08	3·13	...	4·57	5·26	15·2	2	2	1	...	13	14	23
VIII ...	·77	·79	·87	...	...	·92	·94	4·18	6.18	3·06	...	...	5·28	13·0	2	1	2	...	...	13	21
IX ...	·80	...	...	...	...	·90	...	4·09	...	...	...	...	4·68	...	1	...	...	...	...	...	...
X ...	·80	...	...	...	...	...	...	3·64	...	...	...	...	...	...	2	...	...	...	...	...	...

and fibre strength indicate variations among pickings. Generally speaking there is reduction in these characters in the last pickings. The data in respect of seven pure lines grown in different Agricultural Research Stations are presented in table 23.

(6). *Variation between first and second flush of bolls.*—In the normal pickings the quantity of good kapas is more than in summer pickings. A comparison between the good kapas picked in normal and abnormal seasons showed the following differences.

Normal minus summer pickings.

Property.	Difference.
Seed weight (mgms)	8.1
Lint weight (mgms)	18.0
Ginning percentage	5.8
Mean length (inch)	0.080
Fibre weight per cm. (10^{-6} gm)	0.160
Standard fibre weight (10^{-6} gm)	0.183
No. of fibres per seed (1000s)	1.990
Mature fibres%	1.14
Immature fibres%	1.59

Summer pickings exhibit considerable deterioration in quality excepting in fineness and maturity as compared with the normal pickings. Age of the plant and damage by insects are mainly responsible for the deterioration in later stages. Probably higher temperature which prevails during summer is also responsible for this deterioration.

(7) *Variation due to irrigation.*—In an experiment where the plants were given varying doses of water, the fibre qualities showed variation. It was found that (1) the lowest supply of water tends to reduce the mean fibre length to a small extent, (2) the uniformity of fibre length appears to be less in plots with no irrigation in the field (this is not confirmed in pot experiments) (3) there is hardly any variation in fibre weight, and (4) there is no variation in fibre maturity.

(8) *Variation due to spacing.*—Three spacings were tried and the results are presented in table 24 below.

TABLE 24

Property.	Spacing.		Broadcast.
	4″	9″	
Mean length (inch) ...	0·93	0·93	0·92
Mature fibre	52·1	48·6	51·1
Immature fibre ...	17·2	20·6	17·0

It is seen from the table that spacing had no influence on the fibre properties.

(9) *Variation due to rotation.*—Co2 strain of cambodia cotton was tested under six rotational treatments in which the preceding crops were ragi (*Eleusine Coracana*), Cumbu (*Pennisetum typhoides*), Cholam (*Sorghum sp*) Groundnut (*Arachis hypogæa*) Sunnhemp (*Crotalaria juncea*) and in the sixth case fallow. In this experiment the rotational treatments had no significant effect on fibre maturity.

(10) *Variation due to manurial treatments.*—Five experiments have been studied in this connection. The experiments were conducted in three different places and the data are presented in the following table 25.

The differences between manured and unmanured samples are negligible or insignificant except in experiment 4 in which the unmanured samples have significantly higher maturity than the manured samples. It appears that the effect of manures varies in different cases changing with the variety of cotton, soil fertility and conditions of growth.

TABLE 25.

Place of experiment.	Experiment No.	Cotton strain.	Mature fibres.		Immature fibre.	
			Manured.	No manure.	Manured.	No manure.
Hagari ...	1	H1	1·8	92·5	4·2	4·2
	2	H1	89·1	88·2	5·9	6·5
Coimbatore.	3	Co2	42·6	43·4	42·1	40·2
	4	Co2	41·1	49·0	47·9	40·1
Koilpatti ...	5	C-7	69·8	76·1	13·3	11·7

(11) *Variation caused by change of places and season.*—Variations caused in the characters of a pure line due to the crop being raised in Coimbatore and Srivilliputtur were studied. The following are the main conclusions:

(1) At Srivilliputtur, fibres are longer, finer, more mature but lesser in number on the seed than at Coimbatore.

(2) The maturation period of boll and lengthening and thickening phases of fibre are less at Srivilliputtur.

(3) The rate of length development and that of secondary wall deposit are higher here.

(4) The improved length and fineness of fibres and reduction in their number per seed at Srivilliputtur appear to be caused by higher temperature and solar radiation at Srivilliputtur.

The data are presented in table 26.

TABLE 26.

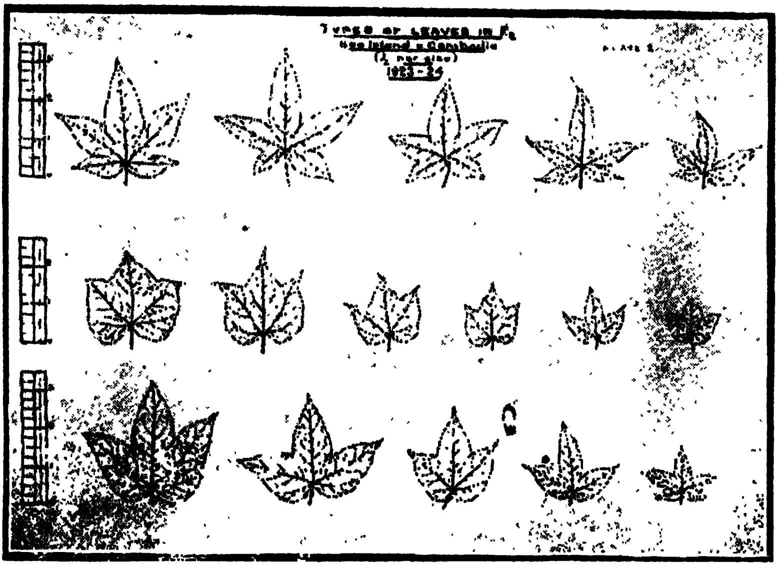
DIFFERENCE BETWEEN SRIVILLIPUTTUR AND COIMBATORE.

	1935–36.		1936–37.		1937–38.		1938–39.		1939–40.	
	Differ-ence.	Signifi-cant.	Differ-ence.	Signifi-cant.	Differ-ence.	Signifi-cant.	Differ-ence.	Signifi-cant.	Differ-ence.	Signifi-cant.
Seed weight in mgm.	0·42	N.	—10·5	S.	1·71	N.	1·67	N.	—4·38	N.
Lint weight in mgm.	6·54	H.S.	9·42	H.S.	12·3	H.S.	12·11	N.S.	15·88	H.S.
Ginning Percentage	2·55	H.S.	5·68	H.S.	4·21	H.S.	4·33	H.S.	7·25	H.S.
Fibre length in inch	—0·114	H.S.	—0·140	H.S.	—0·051	H.S.	—0·116	H.S.	—0·086	H.S.
Fibre weight per cm. in 10^{-6} 6 grm. ...	0·086	H.S.	4·046	N.	0·130	H.S.	0·123	H.S.	—0·012	N.
No. of fibres for seed in 000's ...	2·18	H.S.	4·68	H.S.	2·58	H.S.	3·71	H.S.	6·56	H.S.
Mature fibre %	5·29	N.	—7·9	S.	—5·0	H.S.	—12·1	H.S.	—18·25	H.S.
Immature fibres %	—5·26	S.	9·55	H.S.	—1·96	S.	6·3	H.S.	—10·25	H.S.

H.S. = Highly significant. S. = Significant. N. = Not significant.

4. Autogenous variation.—*Variations which arise due to changes in the genotype are termed autogenous variations.* These variations may arise due to (*a*) Mendelian recombination of genes (*b*) Mutation.

(*a*) *Mendelian recombination of genes.*—Homozygous types breed true to their characteristics and the variations found in them are largely due to environmental factors. If the different homozygous types breed true to their parental characteristics, the evolution of new types becomes impossible. Therefore Nature has provided chances for variations to arise genotypically so that new types of organisms may be continually evolving. In F_2 generation of a cross, segregation and independent assortment of genes take place and hence variations appear in that generation (Fig. 48, 49). These variations



(*Photo from Cotton Specialist.*)

Fig. 48.—This figure illustrates the wide variation that arises in F_2, by recombination of genetic factors.

have chance to occur largely in plants subjected to out-crossing. Therefore in cross-pollinated crops, there are a large number of individuals, heterozygous for many genes.

The mechanism of heredity has been dealt with in the early chapters of this book. New characters arise by interactions between the factors *e.g.*, Walnut comb type in fowls appears due to the interaction between the factors for ' rose ' and ' pea.' Two erect types of groundnut when crossed give rise to spreading type. New varieties and races may be established by the selection of homozygous types for the new characters. In some instances the desirable type may prove to be heterozygous as in the case of Andalusian fowl and the Punjab hairy lintless (PHL) cotton. In the latter case, the short linted type is an heterozygote.

Hybridisation has immense potentialities for variability. When dominance is complete the following possible combinations occur.

Fig. 50. *Cicer gigas*, a new species by mutation in *C. arietinum*.
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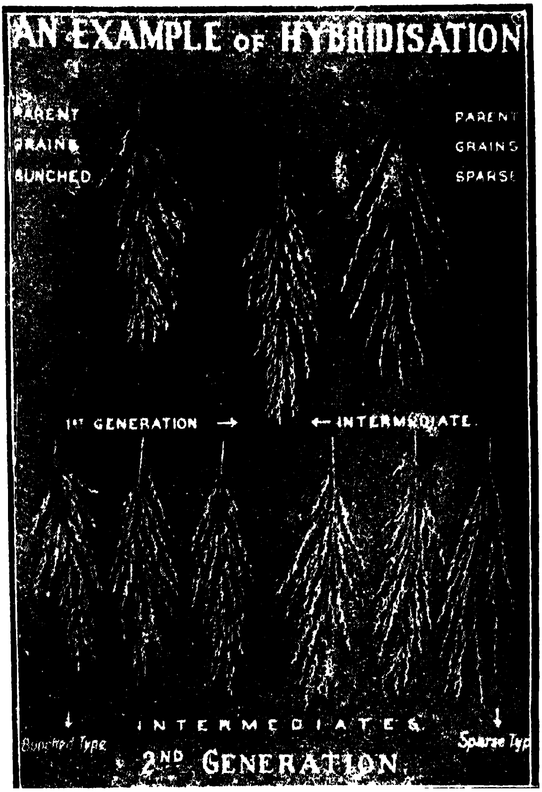
(To face page 111)

Types of gametes	2^n
Gametic combination	4^n
Phenotypes (in the case of complete dominance)	2^n
Phenotypes (in the case of incomplete dominance)	3^n
Genotypes	3^n
Homozygous types	2^n
Heterozygous types	$4^n—2^n$

n = number of factors involved.



(*Photo from Paddy Specialist*).

Fig. 49.—Another example to illustrate the variability of F_2 population due to recombination of genetic factors.

When n = 10, for example, the types of variations involved are very large. The evolution of new strains by crop breeders is largely based on selection from populations in which variations are naturally existing or are artificially induced by hybridisation.

Most of our cultivated crops have originated by hybridisation between different species or varieties. New forms arose not only by recombination of factors but also by changes in chromosome structure. These changes are discussed in a later chapter.

(*b*) *Mutation.—Sudden and discrete change in the gene itself is termed gene mutation.* Allelomorphs have originated in this way.

A large number of desirable genes and members of an allelomorphic series may be distributed in different individuals of the same or related species. Hybridisation between these bring them together. Interaction of factors may bring in an expression of new character. Mendelian variations are therefore caused by the introduction of a new member of the allelomorphic series or by interaction of factors. A change in the environment may demand entirely new characters to adapt the organism to the changed conditions. New genes for the purpose may arise by mutation. The importance of this type of autogenous variation was first pointed out by DeVries in 1900. A large number of mutations have been noted in crop plants since then, though, in comparatively few instances only they proved to be of economic importance. It is now known that mutations take place in genes with comparatively small effects.

Mutations may affect individual genes only when they are termed point mutations or gene mutations. Sudden changes in the characters may also arise by changes in single or whole set of chromosomes.

Mutations in genes are infrequent and therefore the chances for more than one gene to mutate simultaneously are very rare. The mutated form may show large or small differences from the original form. The characters affected may be from gross changes in the morphology to fine distinctions in the physiological reactions. Sometimes mutations give rise to new species by single step. In *Cicer arietinum* a mutant was noticed and it deserved a new species status and hence has been named *C. Gigas* (Fig. 50.) In groundnut from the progenies of a cross between A. H. 32 and A. H 17, the bunch and spreading forms respectively of *Arachis hypogaea*, a gigas type was noted. It deserved a new status and hence has been named as *A. hypogaea Var. gigantea.*

5. Graft hybrids and Chimeras.—Mutation generally occurs in the gametes When it occurs in the vegetative tissues of the plant, it reveals itself in the progeny if such tissue gives rise to gametes. Otherwise the progenies are normal. There are instances where a tissue of a plant may differ in its genotype from the rest of the tissue system of the same plant. Such a plant is termed *graft hybrid* or *chimera.* These chimeras generally arise in grafts between two plants where at the point of graft union, the tissues of stock and scion get mixed up and a branch arising from such a mixture of cells shows mixed characters. Chimeras may also arise from normal plants without grafting. The somatic cells mutate and give rise to new tissues whose genotypes may differ from that of other tissues. Variegated appearances result on account of the differences in the development of chlorophyll and anthocyan pigments.

In this connection, the position of the meristems from which the different permanent tissues develop must be remembered. The outermost single layered *dermatogen* gives rise to the epidermis, the *periblem* gives rise to the ground tissue and the *plerome* to the vascular tissues ; the stamens and pistils and the corresponding gametes arise from sub-epidermal tissues. When the

epidermis forms the mutant tissues, the sexually reproduced progenies may be normal, because the gametes are from sub-epidermal tissues.

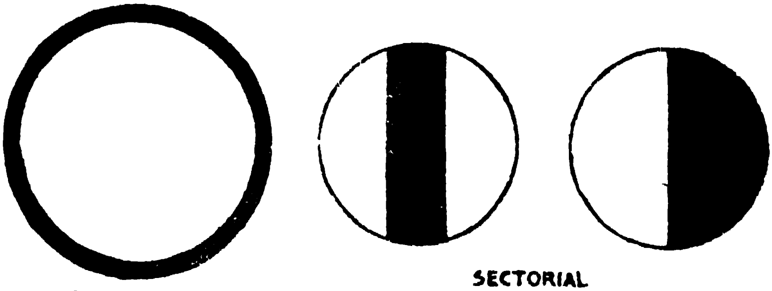


Fig. 51. Diagram to illustrate chimera. The shaded tissues are genetically different from the unshaded tissues.

Based on the distribution of the genotypically differing tissues, chimeras are of three types (1) *sectorial chimera* (2) *periclinal chimera* and (3) *hyper-chimera* (Fig. 51).

By grafting tomato (*Lycopersicum esculentum*) on to night shade (*Solanum nigrum*) and *vice versa*, Winkler produced chimeras. When the graft unites at cut surfaces, it is again cut across the point of union and fresh buds are encouraged to grow from the cut surfaces. At the union of stock and scion, the tissues of the two are found mixed up and depending upon the region from where the new bud arises, the chimera may be sectorial or periclinal. The results of cutting at the graft union in different types of grafts are shown in 1, 2, 3 (Fig. 51). Depending upon the position from where the new bud arises, in the shaded or unshaded positions, in the figures, the chimera will vary. Where the different tissues occupy different sections of the plant in stem, leaf, etc., it is termed *Sectorial chimera.* In this case, the tissues do not surround each other.

If the new bud at the cut surface arises from sub-epidermal tissues in such a way that the surrounding tissues are of one type and the internal tissues are of another type, just as the glove surrounds the hand, then the chimera is *periclinal.*

In chilli (*Capsicum annuum*) seeds were treated with aqueous solution of colchicine for producing polyploids. Out of 244 plants from the treated seeds 54 were tetraploids, 4 were periclinal ploids—chimeras with 4n epidermis and 2n pollen and 186 were diploids. The progenies of the ploid chimeras were normal plants because the epidermal cells alone showed 4n chromosomes and the sub-epidermal cells showed 2n chromosomes. Since the gametes are formed from the latter, the progenies are normal diploids.

In certain cases, the two types of tissues may grow mixed together, so that the different cells instead of occupying definite regions may be scattered in the tissues. These are termed *hyper chimeras.*

When propagated by seeds, chimeras do not breed true to chimerical characters. This is to be expected because the gametes are formed from sub-

epidermal cells and the seeds follow the genotype of these latter. Similarly, propagation through root cuttings behave uniformly true to the genotype of the internal tissues because roots are endogenous in origin unlike the branches. In the case of hyper chimeras the progenies will be variable when multiplied either through seed or root cuttings.

The following is an example of chimera in rice spikelets. In one type the glume was wholly purple and in another, the glume was green with purple tip. When the two were crossed the former was dominant over the latter. In one progeny of the cross, a plant was met with wherein the full purple and the green glumed spikelets, which ought to occur normally in different plants, were occurring together in the same panicle. The grains from the panicle were separated into green and purple and sown separately. The green glumed grains occurring in purple glumed plant, behaved just like the purple glumed grains in that they segregated, whereas the green grains from the normal green plants breed true. The segregation of green glumed grains is shown in table 27.

TABLE 27.

Green glumed grains from panicle number.	Segregation into	
	Purple glumes.	Green glumes.
1	20	16
2	7	3
3	10	7
4	30	12
	67	38

The colouring matter is confined to the cells of epidermis which bear homozygous recessive factor while the embryo inside is heterozygous.

A case of ploid periclinal chimera in chilly has been referred to. The haploid sectorial chimera from the cross *Brassica Campestris* (n—10) × *B. nigra* (n—8) showed n—18. This haploid—diploid chimera has evidently arisen from a hybrid seed with n—18 and on treatment with colchicine, a section of the progeny was doubled in chromosome number.

6. Parallel variation.—Variation and selection in nature have given rise to multiplicity of varieties and species. If one could have a record of all details regarding the evolution of all the cultivated plants, the ancestry of many of them could be shown. Variations in divergent lines may have widened the differences between many forms and as a result, in modern taxonomy, they have come to be placed in different species or even genera. These related genera and species bear many characters common between them or at least they bear close resemblance to one another in respect of some characters. Detailed studies are likely to show that in the course of development of similar characters there are many developmental steps common between them. In other words, the developmental processes run on parallel lines, though ulti-

mately there may be small or large differences in the phenotypes. The closer the individuals on the taxonomical scale, the greater the resemblance between them and the variations that exist between such types are termed *parallel variations.*

The fact that in development and appearance, characters in related types bear closer resemblance suggests that the corresponding genes also must be alike. In such of the organisms where genetic analyses of the characters in the related species have been carried out, homology of the genes has been noted. In Chapter XII, the species relationship in cotton has been discussed. It shows the parallelism in the genotype of the different allied species. The factor R and its allelomorphs cause pigment development in the various cottons, though there are slight differences in the expression of the factor in the different species. It forms a multiple series in the Asiatic and American cottons. In the American group there are no modifiers to enhance its expression and hence it is weak. In the Asiatic group, it causes red plant body, red flower and intense petal spot while in the American group it causes weak expression in plant body and flower but no spot in the petal. The homologous organs may be governed by the same kind of genes or different members of a multiple series or by different sets of modifier complexes. Therefore, while development and function may remain the same in homologous organs, they may be governed in expression by different genotypes.

Maize and teosinte are allied plants though morphologically they are widely different. Genic analyses have shown that at least 28 genes are common between them.

Branching habit is dominant over non-branching in groundnut. This is generally the case in many of the leguminous plants and it suggests homology and parallel variation in the group.

Study of parallel variations in the world collection of plants by Vavilov has led that Russian botanist to enunciate the principle of homologous series in variation. This is similar to the periodic table in chemistry where grouping of the chemicals based on atomic weights, enables chemists to predict the properties of missing elements. By a study of variation in the existing types of plants it is possible to predict a few missing types. The recognition of parallel variation in plants indicate the degree of relationship between them and probably may be of advantage in utilising such types for crossing in plant breeding. Wheat, rye and *Aegilops* show parallel variation and hybridisation between them has been carried out with advantage.

In some instances, unrelated species may bear close resemblances in respect of certain characters. This is termed *mimicry*. This has been widely studied in the case of butterflies and moths. This problem has received very little attention from botanists. In *Orobanche*, the seeds closely resemble those of tobacco and hence when they are mixed up it is difficult to separate them. A striking case of mimicry was reported by Vavilov in the case of cultivated lentil and the weed vetch. In both the cases there are varieties which differ in seed characteristics. In growing the lentil, the ryots sorted out the seeds before sowing and eliminated vetch. One difficulty was met with in

the process. There were types of vetch whose seeds very closely resembled those of lentil and hence separation was not practicable in such cases. The resemblance between the two was not only in respect of seed characters but also in their growing and fruiting periods. The mimicking type of vetch thus could not be eliminated from lentil.

Mimicry is not due to slow accumulation of genetic factors favouring resemblances. It is due to Natural Selection which favours mimicking types which may arise even by a single step or sudden variation.

7. General.—Plant breeders are mainly concerned with improving the economic characters of crop plants. The needs of men are so varied that the work of a plant breeder may cover many aspects of life. It may concern the food grains, textile fibres, chemicals and drugs, dyes and many other vegetable products which it is impossible to list here. The character concerned in the economic utilisation may be one of morphological, anatomical or physiological variability. For selecting the best type the breeder may have to consider and measure these morphological, anatomical or physiological characters. After making the measurements, the variations due to environment and those due to genotype must be properly adjudged. The problem is one of selecting the individual with the highest value and it should breed true. Leaving apart the variations caused by genetic interactions and modifiers, the types and causes of variations met with in economic characters are so varied that it is impossible to give a comprehensive review here in respect of all crops. The variations met with in the fibre properties in cotton have been discussed in this chapter to show the variations in quantitative characters.

Chapter 9

MUTATION

MUTATION—DE VRIES AND MUTATION—GENE MUTATION —MUTATION RATE—THE NATURE OF GENE MUTATION—EXPRESSION OF MUTANT FORMS—MULTIPLE ALLELOMORPHS—THERMOCHEMICAL EFFECT ON MUTATION—IRRADIATION AND MUTATION—HERITABLE VARIATIONS BY IRRADIATION AND THERMO CHEMICAL TREATMENTS—MUTATION AND EVOLUTION.

1. Mutation.—Developmental variations are short lived in their effect in that they are not truly transmitted to the progenies. Mendelian laws relate to variations that may arise through hybridisation between individuals differing in character pairs. These explain variations due to recombination of existing factors only, but offer no explanation as to how variations in the genes arise. This latter consideration becomes important in discussing evolution of new types. Until 1900, the problem of evolution was widely discussed but the hypotheses were based on manifested characters without reference to the genetic differences between them. Now it is known that the transmission of characters from parent to progeny largely depends upon genotype only with cytoplasm and outside environment causing fluctuating variations. The discovery of the hereditary mechanism calls for reconsideration of the old conceptions in the light of new discoveries. Darwin in his theory of organic evolution opposed Lamarckian principle but still he could not explain the origin of new variations and through his pangenes conceded a little to Lamarckism by assuming that some of the acquired characters are inherited. DeVries (1900) provided the necessary explanation out of this difficulty by recognising mutation as providing the necessary change in genes in the course of evolution. Mutation has been discussed in brief in the preceding chapter and it has been pointed out that mutation refers to sudden discrete and discontinuous variations that are found in otherwise pure breeding populations. Predecessors to DeVries considered variations to be continuous and consisting only in small steps, but the studies of DeVries in *Oenothera* showed that variations involving large differences may also arise.

2. DeVries and Mutation.—Discontinuous variation was suggested by Bateson (1894) and Kosschinsky (1899). They did not realise the significance of the same but DeVries pointed out its importance in evolution. In 1886 DeVries noted wild plants of *Oenothera Lamarckiana* near Amsterdam. He noted two varieties in them—*brevistylis* and *laevifolia.* He collected seeds and raised a total population of 54,343 plants in several generations and isolated 834 mutants that fell into seven types. These, DeVries considered as new species. According to him the differences in the mutant arose by a single change in the germ which he termed as mutation. Later studies showed that the mutations noted by DeVries belong to complex types. Some of them were changes in a single gene and others were due to changes in whole chromosome or set of chromosomes. The latter refer to structural changes or in

number in the chromosome complement of a cell. In this chapter gene mutations are discussed.

3. Gene Mutation.—Comprehensive knowledge of mutation is now possible only through the extensive studies carried on *Drosophila* flies by Morgan and others. In studying gene mutations certain precautions in technique are necessary because faulty technique does not enable valid conclusions to be drawn from them.

The material in which mutations are noted must be pure breeding and it must come from a line that has been carefully selfed for a number of generations. If the plants are cross fertilised, they are likely to be heterozygous and the new variations noted in them may be due to segregation and not to mutation. To observe new mutations, the population must be very large because the frequency of mutations is so small that they are not likely to be noted in small population.

The new variations observed in a homozygous population may fall into any one of the following groups : (1) non-heritable modifications (2) plasmatic enduring modifications (Dauer-modifications) (3) gene mutation (4) chromosomal aberrations. Each type must be tested by suitable experiments.

When the effects of X-ray and radiations on living cells were announced, a large number of tests on plant cells were carried out especially by Guillermont (1908) and Gager (1908). In earlier works no attempts were made to analyse genetically the effect of irradiation. Muller was the first to carefully plan out experiments with *Drosophila* the genetics of which was well studied in Morgan's laboratories. Muller (1928) found that X-ray increased mutation rate by at least 150 times the normal one.

Later experiments showed that short wave radiations as the rays of radioactive substances, the X-rays of different wave lengths, and ultra-violet rays may also induce mutations. These discoveries are useful in that they offer

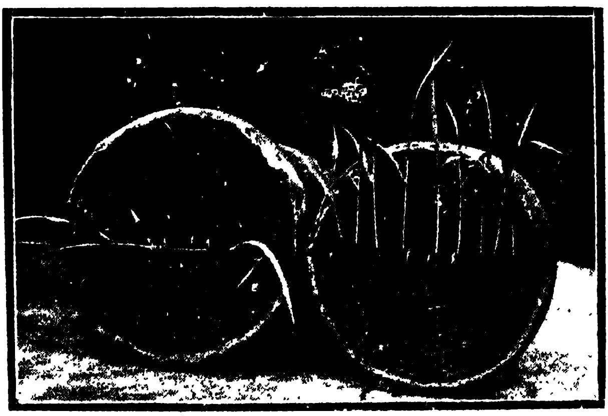


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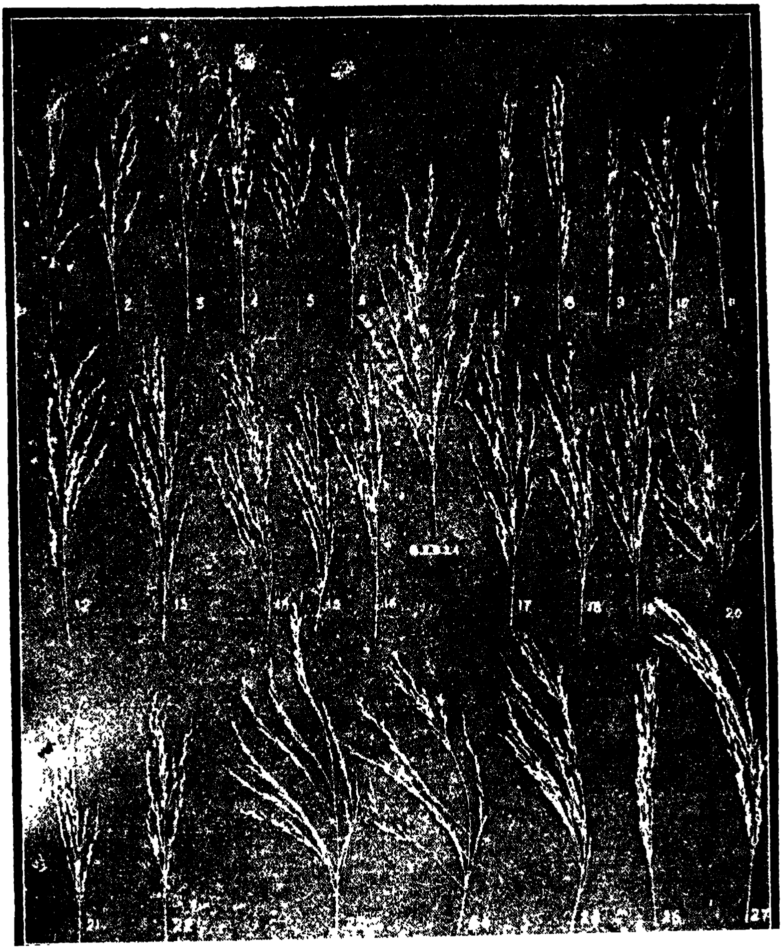
Fig. 52.—Ageotropic mutant from the pure line CO. 4. On the left is the mutant which is straggling horizontally and on the right is the normal plant.

scope for artificially inducing mutations in the laboratories. Such induced mutations may be genetically studied and their economic utility may be exploited. *The discovery of the possibility of artificially inducing mutations has come in as a handy tool to geneticists.*



(*Photo from Paddy Specialist*).

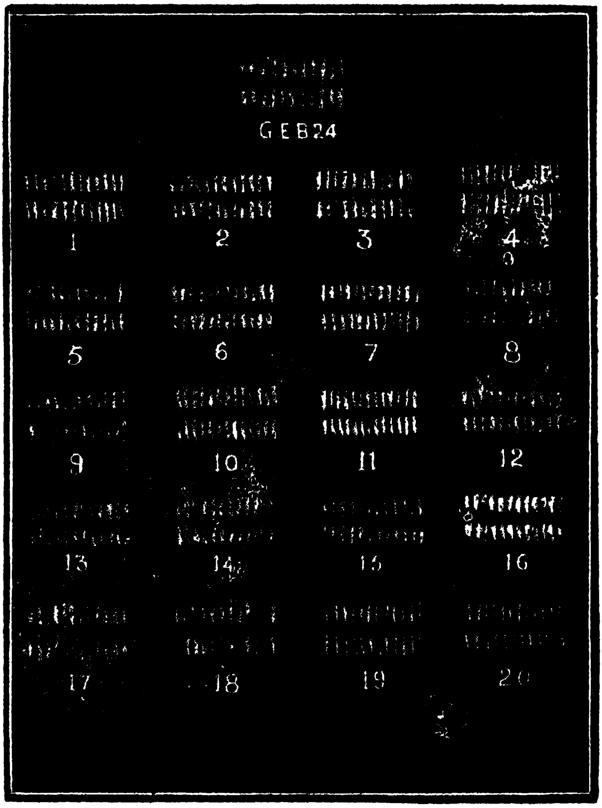
Fig. 53.—Variations in the panicle induced by X-ray irradiation of the seeds of the pure line G. E. B. 24.

Detailed work has been carried out on *Drosophila* but work on many plants has also been reported in the last few years. The following are a few examples.

Oat, wheat, barley and maize : (Stadler).
Cotton (Horlacher and Goodspeed).
Nicotiana (Goodspeed).
Datura (Blakeslee).
Tomatoes (Lindstrom).
Rice (Parthasarathy).
Millets (Rangaswamy Ayyangar).

All these experiments showed the general effect of short waves on the genes of living cells.

In stocks of *Drosophila* flies breeding true to type an occasional variation in respect of a character was noticed. This change could not have occurred by Mendelian segregation, since the variant was not found in the near ancestry of the stock and out-crossing was prevented by experimental conditions. The mutant character was subject to genetical analysis. It was found, for example, in a stock of flies with white eyes (W), a few flies with ivory colour arose and by breeding tests it was found to be governed by a factor w_1, allelomorphic to W and recessive to it. This new factor w_1, could have arisen by the factor W suddenly changing to it. This is an instance where a single gene has changed.

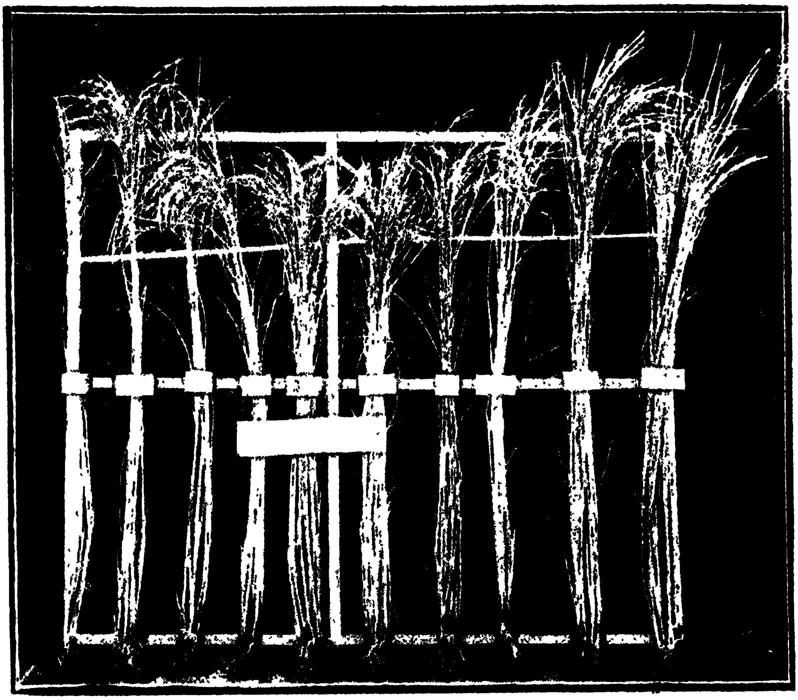


(*Photo from Paddy Specialist*).

Fig. 54.—Variations in the grains of the pure-line rice G. E. B. 24 arising due to X-ray irradiation of the seeds.

Later studies in crop plants revealed that gene mutations are possible in them also. A large number of them pertaining to different characters have been recorded. The mutation may be in regard to physiological, anatomical or morphological character of the plant as shown below :

Rice—In a population of pure breeding erect type of improved strain Co_4, ageotropic form arose by mutation of factor *La* to *la*. Figs. 52, 53, 54 and 55 show the mutant forms which arose in the progenies of X-rayed seeds of the pure line rice, G. E. B. 24.



(Photo from Paddy Specialist).

Fig. 55.—Mutations affecting height of plants, induced by X-ray treatment of seeds of the pure-line G. E. B. 24.

Cholam—In a population of green stemmed plants, purple veined type arose by the factor *Mtb.* mutating to *mtb.* In the mutant, purple colour is developed around the vascular bundle.

Cumbu—The following mutations appeared due to X-ray irradiation : weak mid-ribbed plants, male sterility, gappy panicle (Fig. 56), forked panicles (Fig. 56), goose necking, tip sterility and chlorophyll deficiencies.

Ragi—Chlorophyll deficient types in which first 2-3 leaves were white banded while mature plants were green ; in two mutants the panicles were affected (Fig. 57).

Cumbu threw out more mutations than ragi showing that the former is diploid and the latter tetraploid.

Cotton—In normal types of flowers in Asiatic cottons, petalody arose by the factor *Pdy* mutating to *pdy*.

4. Mutation rate.—In *Oenothera* DeVries found that only 1.5 % constituted the mutants. *The characteristic feature of mutation is that the mutant breeds*

true. A gene which mutates is stable for a considerable period. Thus, the ageotropic mutant breeds true to that character which means that *the mutated*

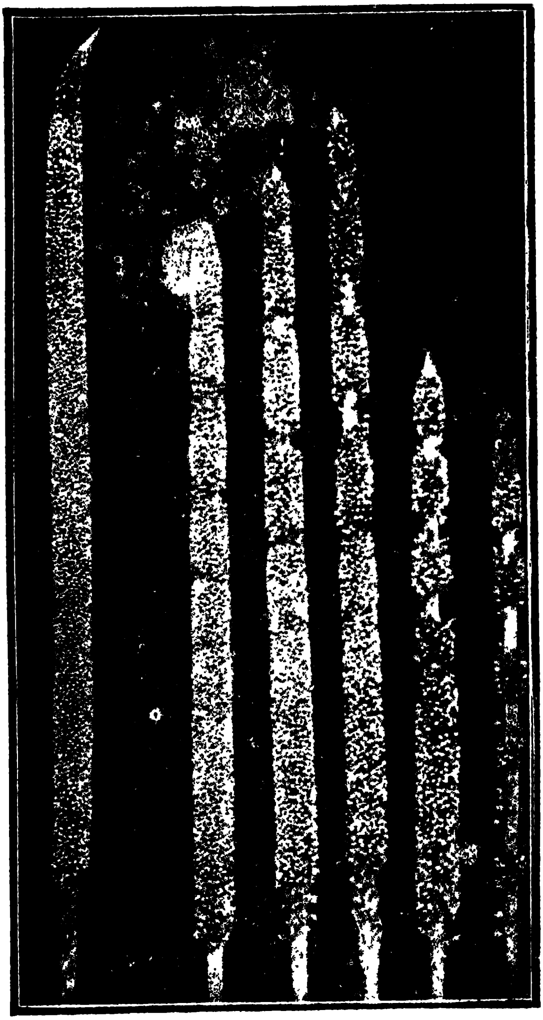


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Fig. 56.—Gappiness in the ear head of pearl millet, *Pennisetum typhoides*, induced by X-ray.

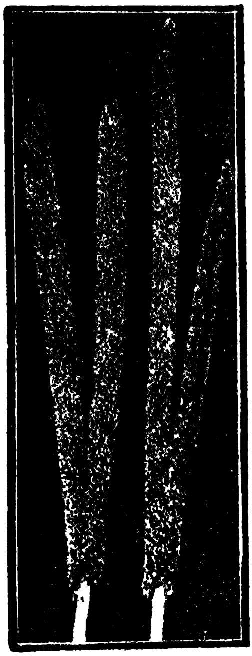

Fig. 56.—Forking in the ear head of pearl millet, *Pennisetum typhoides*, induced by X-ray.

gene has stability like other normal genes and it truly reduplicates itself during cell division. This constitutes one of the extraordinary properties of the genes in that it combines two opposing properties viz., (1) *stability* (2) *a change from the stable condition, and stability of the changed condition*. The physico-chemical basis underlying this is not yet completely understood. Mutation is generally observed in a single gene at a time and the occurrence of mutation simultaneously in more than one gene is extremely rare.

Johannsen's pure line theory shows the high degree of stability of the gene. A zygote divides millions of times before the adult is developed and according to pure line theory the homozygous population breeds true generation after generation without any change in the genotype. During all this

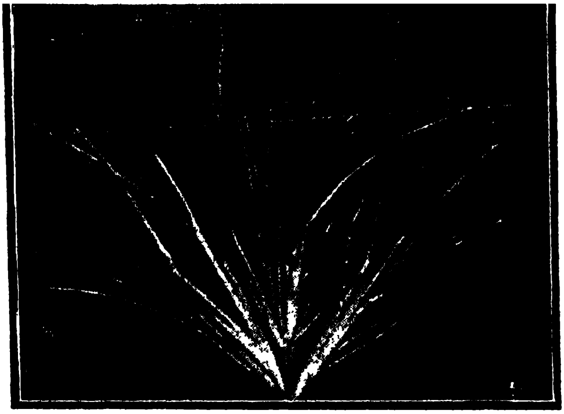

Fig. 57.—Fasciation of spikelet in ragi, *Eleusine coracana* induced by X-ray.

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period the cells divide billions of times and yet the genes do not change. In *Drosophila* the gene stability is calculated to be of the order of 100,000 years *i.e.*, one mutation may occur in a population of 1,000,000 individuals. Haldane and Penrose report in respect of two loci, which mutate in 100,000 generations *i.e.*, in about 3,000,000 years. In maize, Stadler reports values ranging from thousands to millions of years.

TABLE 28.

Frequency of spontaneous mutation in genes of maize.

Gene.	Gametes tested.	Mutations.	Mutation per million.
R	554,786	273	492
I	265,391	28	106
Pr	657,102	7	11
Su	1,678,736	4	2·4
Y	1,745,280	4	2·2
Sh	2,469,285	3	1·2
Wx	1,503,744	0	0

If mutation is considered as a mis-step in its reduplicating itself during cell division, the mistake occurs only once in a million steps. This means that the gene has attained a high degree of precision in manufacturing its own type.

5. The nature of gene mutation.—Gene is the basis for development of a character and mutation is the basis for variation in the same. Mutation does not alter the capacity of the gene to reduplicate itself. The size of the gene is of the order of a complex protein molecule. The capacity for a mutated gene to reduplicate is taken as a proof for its being a single unit. Since it is very rare that two genes mutate simultaneously, mutation in one gene does not affect even the immediate neighbour, even if the latter happens to be identical with it. Therefore mutation appears to be of the order of micro-chemical accidents. "*When the molecular or atomic motions chance to take a particular form to which the gene is vulnerable, then the mutation occurs*". (Muller)

Genes are hypothesised to be complex molecules like proteins. They are separated from one another in the chromosomes by non-genic material, or inert regions. Gene multiplication is not by fission of the swelled gene as it happens in the multiplication of yeast cells. A new gene, exactly identical with the present one is built up by the side of the old one. This property of *autocatalysis* is not evident in any other type of chemical or physical changes in non-living matter. *In this autocatalysis, a type of auto-attraction is maintained.* The latter is evident even after gene mutation, so that the mutated gene, which is present in the same locus, is still an allelomorph of the old gene.

It is found that mutation is most frequent in mature sperm cells and least in other cells. If mutation is considered as a mistaken reduplication during cell division it must be most frequent when cell division is at the maximum frequency. But that it is not so shows that mutation is not a mistaken reduplication but a change in the genic structure which latter is faithfully reduplicated. Identical genes do not mutate simultaneously. *This shows that mutation is not directed by external environment but is a property of the gene itself.*

It was once thought that mutation involves loss of genes. Since reversible mutations are known, *mutation cannot be loss of entire gene, but only a change in the genic structure.*

6. Expression of mutant forms.—In plants the gametes are formed from cells beneath the epidermis. Therefore, for a mutation to be successfully reflected in the progenies it must arise in cells from which the gametes are formed. In most cases, the mutated gene is recessive to the normal *wild type* and therefore is *hypomorphic*. *Since only one gene mutates at a time, the cell, after mutation, is heterozygous for the mutated gene pair.* Generally the mutations appear so late in the development of the individual that during meiosis a few gametes with the mutant genes are formed. The chances for the gamete with the mutated gene to mate with another one with the same mutated gene are rare but it generally mates with the normal one. Thus the progeny is heterozygous for the same and this segregates in mendelian ratio in the next generation. Dominant mutations are rare, and these when present express themselves immediately after mutation.

In plants there are many growing points. If mutation occurs in any one of these actively dividing meristematic tissues, the branch arising from them, expresses the mutant character if it is dominant and this phenomenon is known as *bud mutation.*

As already referred to, mutation may affect any of the characters of the plant. Every gene is susceptible for mutation though there are considerable differences in their mutation rate. In the examples considered in section 3, in the ageotropic mutant in rice, the mutation affected the habit and reactions to geotropic stimulus. In cholam it has affected the pigmentation around the vascular bundles. In petalody of cotton, the normal development of stamens is changed to petaloid structures. Mutations in morphological features are much fewer than those which are not so prominently expressed. Since mutations are generally degenerative, a large number of them prove lethal at various stages of development. There are other types of mutations which show very small visible effects and they are difficult to detect. Certain mutations may not have phenotypic effect at all as they may pertain to small physiological reactions inside the plant. There are others which affect genes themselves, *e.g.*, in maize the gene for white pericarp has mutated to an allelomorph termed "*ever-sporting*". Here the normal and the 'ever-sporting' genes differ in their mutation rate only without any difference in the phenotype. *In Drosophila it was found that lethal mutations constitute 5 to 10 times the visible mutants and the former constitute half to one-third the mutations that occur without any visible effect at all.* It is likely that still larger number of mutations occur which could not be detected. In *Drosophila*, some of the mutations were found to be reversible. These mutations with small effects are found to be of greater importance in evolution than those with large effects because the former tend to produce smaller disturbances in the development of the organism which the plant can survive while mutations with large effects tend to produce large disturbances in the development.

Mutation has immense potentialities to produce variations in different directions in any particular character. Yet the mutations do not proceed in all directions but are restricted in their scope as pointed out by the law of homologous series in variation. The various genes found distributed over a number of related species and geographic areas are essentially similar so that the developmental processes involved in homologous characters are also similar. It is on this principle that in symbolising genes of crop plants it is

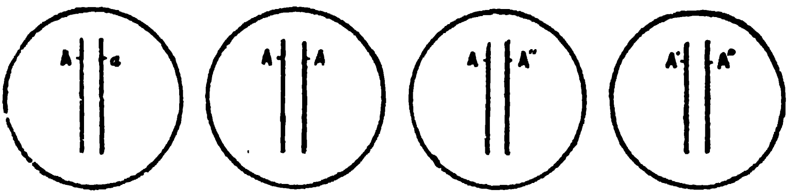


Fig. 58.—Diagrammatic representation of multiple allelomorphs. A mutates into its allelomorph a. It may further mutate to A^{I}, A^{II}, A^{III} etc., Being allelomorphs, A, a. A^{I} and A^{II} occupy corresponding loci on homologous chromosomes as shown in the diagram. In any diploid, only two members of the series can be present as shown above.

desirable to adopt the same basic letters for denoting similar characters, *e.g.*, v and w denote virescent and albino chlorophyll deficiencies in maize, rice and cholam to show that ultimately their homology may be established.

7. Multiple allelomorphism.—*Allelomorphism arises by the same gene mutating to other forms* (*Fig.* 58). Thus, for example, the factor for narrow leaf in cotton (L) by mutating forms broad leaf (l).. The two factors being situated in the same locus, segregate in 3 : 1 ratio in a cross. If, for example, the same factor L mutates to forms in different instances, variations in the same character arise but all mutated genes are in corresponding loci on different homologous chromosomes and hence form an allelomorphic series. Thus, the factor L has mutated to L^B (mutant broad), L^L (laciniated) and L^I (mutant intermediate). These different grades of leaf lobing arise by the mutation of a single factor L and hence are termed " multiple allelomorphs ".

In a cross involving the different leaf shapes, monogenic differences are observed between any two pair.

$LL \times ll$ — 3 : 1 in F_2
$L^BL^B \times$ ll — 3 : 1 in F_2
LL $\times$ LL^{BB} — 3 : 1 in F_2
LL $\times$ L^IL^I — 3 : 1 in F_2

This is expected because L, L^B, L^I and l are at corresponding loci. More than a pair of factors cannot enter a cross. This is diagramatically represented in Fig. 58. Similarly anthocyanin pigmentation in the plant body of cotton forms a multiple allelomorph series.

OLD WORLD GROUP :	
Spotted series :	Gene symbol.
Red plant body	R_2^{RS}
Red leaf	R_2^{LS}
Red calyx	R_2^{CS}
Tinged stem	R_2^{AS}
Green Stem	R_2^{OS}
Spotless series :	
Red leaf	R_2^{LO}
Tinged stem	R_2^{AO}
Duplicate	R_2^{GO}
NEW WORLD GROUP :	
Spotted series :	
Red leaf	R_2^{LW}
Tinged stem	R_2^{R} R_2 R_2^{AF}
Spotless series :	
Tinged stem	R_2^{AO}
Duplicate red	R_1^{RO}

When plants showing characters forming the multiple allelomorphic series are crossed, the hybrid shows 3 : 1 segregation in F_2 in respect of that character.

If three or more characters are suspected to form multiple allelomorphic series, a cross between any two shows monogenic difference. Any deviation from this indicates a different relationship between the genes. The following is an example from crosses made in testing allelomorphism of genes for lintlessness in cottons. In 1940 a mutant in Broach I (*G. herbaceum*) was noted at Baroda. The plant was hairy with thick fuzzy seed coat. It is similar to another mutant noted in 1932 in seed material from Viramgam. Baroda lintless was crossed to other lintless types to study the genetic relationship.

(i) Baroda lintless X Broach I linted : F_1 was linted. F_2 showed 96 linted and 29 lintless giving single factor difference.

(ii) Baroda lintless X 1027 A.L.F. and 1027 ALF x Wagad, Darwar, Nagpur, Mollisoni, Punjab glabrous and Nandyal lintless types gave linted F_1. This shows that Baroda lintless is *complementary* to them. In the cross with Punjab hairy lintless (PHL) Baroda lintless gave a lintless F_1. Baroda and Viramgam represent independent mutations at the same locus. The gene is designated as *l*.

There are three other lintless genes in cotton as shown below :

L_{ia},

L_{ib},

L_{ic},

8. **Thermochemical effect on mutation.**—The rate of chemical reactions are increased by rise in temperature. According to Vant Hoff's rule for every 10^0C. rise in temperature the rate of chemical reaction is doubled. If gene is hypothesised to be a chemical molecule in its essential structure and if mutation is a change in the structure of the molecule, it follows that temperature must have influence on this. Timofeeff Ressovsky has shown this to be so. Mutation rate is increased by temperature. By rise in temperature chemical reactions in the neighbourhood of genes increase and these intramolecular disturbances increase mutation rate. Old seeds which have been stored for long time show a greater mutation rate than fresh seeds. In paddy, keeping the grains in cold storage gave rise to mutant forms.

9. **Irradiation and mutation.**—Muller (1927) found that X-ray increases the rate of mutation. The increase in rate was of the order of *hundred* fold or more. X-ray irradiation also had no *directive* effect on mutation as the nature of mutation could neither be controlled nor predicted. *The high energy radiation penetrates the cell and causes an increased chemical activity. Besides this, the chromatin has selective absorbing tendency for these rays and thus X ray increases mutation rate both directly and indirectly.* The effect is not like that of heat on chemical reactions where the heat motions have a general effect in increasing all chemical reactions. X-ray also produces change at particular points only. By an increase in the intensity of irradiation the rate of mutation is increased but the nature of mutation is not altered. Since most of the mutations are degenerative in effect, by an increase in the intensity of irradiation larger number of lethals appear. The quantitative relationship between

irradiation and mutation is linear in that increased dosage increases rate of mutation within certain limits.

The following table shows the dosage relationship of the X-ray on mutation rate in *Drosophila melanogaster*.

TABLE 29.

Dosage in *r* units.	% lethals.
6315	4·71
6316	4·72
6315	4·57
12630	9·75
12632	9·65
12627	9·53
25263	20·22

(after Timofeeff-Ressovsky)

From shortest r-rays of radium to X-rays of 0.01 to 2.0 A, all rays are effective in producing mutations. The action of free high speed electrons was reported by Gager and Blakeslee (1927) in *Datura* and by Stadler (1928-1931) on barley and maize.

There are certain factors which have influence over the production of mutation by irradiation.

(1) Different genes show different rates of mutability. Even the allelomorphs may differ in this respect.

(2) Races and species differ in the rate of mutation in respect of genes in them. Stadler found that in the polyploid species of wheat and oat there was considerable difference in rate of mutation. *Avena brevis* and *A. strigosa* n = 7, *Triticum monococcum* n = 7. These showed higher rates of mutations than *Avena byzantina* and *A. sativa* (n = 21) and *Triticum dicoccum* (n = 14) and *T. vulgare* (n = 21) respectively. The mutation rates are shown in the following table 30.

TABLE 30.

Species.	Chromosome number.	Mutation per unit $\times 10^{-4}$
Avena brevis	7	4·1
A. strigosa	7	2·6
A. byzantina	21	0
A. sativa	21	0
Triticum monococcum	7	10·4
T. dicoccum	14	2·0
T. durum	14	1·9
T. vulgare	21	0

(after Timofeeff-Ressovsky).

The mutation rate is also governed by physiological state of the organism such as age or sex. The following data from *Drosophila* are furnished.

TABLE 31.

Age of sperm in days after X-raying.	% lethals.
1— 5	6·9
5—10	8·3
10—15	7·3
15—20	4·0
20—25	3·1
25—30	1·8
Control	0

Mature germ cells show greater susceptibility to mutation. The latter phenomenon has nothing to do with cell division. *That this is so is indicated by the fact that even dry seeds, in which no cell division is in progress may show mutation when irradiated.* The directness of effect of X-ray is further shown by the fact that mutations appear in the generation following X-raying. Thus in the case of cottons, *G. herbaceum* and *G. arboreum* dry seeds were exposed for 2, 5, 10, 15 and 20 minutes at target distance of 15 cm. employing current of 10 m.a. and 50 k.v. with no filter. Immediate effect of the treatment was to reduce germination as shown below.

TABLE 32.

	% germination after irradiation.		
	G. herbaceum.		*G. arboreum.*
	H. 2405	H. 2919	K. 546
Control ...	91	93	87
Treated 2′ ...	42	78	64
5′ ...	55	74	68
10′ ...	66	58	73
15′ ...	55	75	55
20′ ...	42	54	53

On sowing the seeds one abnormal plant appeared and died. In the next generation chlorophyll deficiencies and meristic variations appeared. This shows that the effect of X-ray is directly on the genes. Further, if untreated chromatin is introduced in treated cytoplasm, the former shows no change. The effect of X-ray is not transmitted from the treated part to the untreated.

Mutations have been induced in crop plants by X-raying dry seeds, germinating seeds, seedlings, anther or ovule. Varied mutations have been noted in different crops.

Paddy.—Wet and germinated seeds were badly affected while in dry seeds lethal effect increased with dosage. Dry seed, seed soaked in water for 24 hours and germinated seeds were irradiated under the following conditions of irradiation. Unscreened exposure under a water cooled Coolidge tube with copper anticathode operated at 53 K. V. and a tube current of 10—11 m. a. at target distance of 17 cm. Exposure time was of 3 grades : 1 hr. 2 hrs. and 3 hrs. Percentage survival in seeds is shown in table 33.

TABLE 33.

Variety.	Seed treated	X-ray.	% Survival.
G. E .B .24	Dry seed	Control	80
		X-ray 1 hour	35
		2 hours	16
		3 ,,	3
	Wet seed	Control	86
		X-ray 1 hour	38
		2 hours.	0
		3 ,,	0
	Germinating seed ...	X-ray 1 hour	11
		2 hours.	0
		3 ,,	0
Co. 4	Dry seed	Control	85
		X-ray 1 hour	62
		2 hours.	4
		3 ,,	5
	Wet seed	Control	79
		X-ray 1 hour	10
		2 hours	1
		3 ,,	1
	Germinating seed ...	X-ray 1 hour	2
		2 hours	1
		3 ,,	2
Korangusamba	Dry seed	Control	82
		X-ray 1 hour	44
		2 hours.	25
		3 ,,	8
	Wet seed	Control	65
		X-ray 1 hour	3
		2 hours	0
		3 ,,	
	Germinating seed ...	X-ray 1 hour	0
		2 hours	0
		3 ,,	0

The data show that wet and germinated seeds are seriously affected by irradiation while in dry seeds lethal effect increased with dosage. Amongst the surviving progenies, mutations affecting stature, size of grain, size of leaf and chlorophyll contents of leaves were noticed. Pollen sterility of varying degrees was evident in most plants. In X_2 generation, chlorophyll content, size of plant and grain and fertility were affected by mutation. In the progeny

of semi-sterile mutant a number of dwarf mutants appeared. Spikelets were small and malformed, pollen was normal but no grains were set. Two other mutants 'stumpy' and 'beaked sterile' did not breed true.

Sorghum.—Pollen grains of *Sorghum* were irradiated for 5, 10 and 15 minutes. Though the pollen grains did not show any significant difference when germinated in artificial media, they were considerably less effective with increased dosage when dusted on selected stigma. Table 34 shows the number of flowers treated and percentage of seed-setting.

TABLE 34.

Duration of exposure to X-rays.	No. of flowers emasculated and pollinated.	No. of seeds set.	% of seed setting.
5 minutes ...	48	20	41·7
10 " ...	39	7	18·0
15 " ...	61	11	18·0

One of the plants from these treated seeds showed suppression of top leaves.

Cumbu.—(*Pennisetum typhoides*) Earheads at flowering time were treated. Average setting in treated earheads was 381 grains while in normal cases it is 1204 grains. When germinating seeds were treated, differences in yield of grain, height of plant and number of tillers per plant were affected.

Cotton.—Effects of treating seeds of cotton were already referred to. When pollen grains were x-rayed, the seeds showed less viability. Some selections from such seeds showed increased yield in the first few generations but later they were disappointing.

10. Heritable variations by Irradiation and thermo-chemical treatments.—The variations due to irradiation or thermo-chemical treatments fall into two main groups : (1) plasmatical changes such as in plastids or dauer modification (2) genotypical changes due to (*a*) *gene mutations* (*b*) *chromosome mutations* (*c*) *Karyotype mutations.* Very little work has been done on cytoplasmic variations due to irradiation. Of the genotype variations gene mutation has been already discussed. Chromosome mutations may fall into any one of the following groups : (*a*) fragmentation of chromosomes (*b*) deficiency and deletion (*c*) duplication (*d*) inversion (*e*) translocation and segmental interchange. Karyotypic variations fall into the following groups : (*a*) Trisomics (*b*) polyploids (*c*) heteroploids. Chromosomal variations and karyotypic variations are discussed in detail in the succeeding two chapters.

11. Mutation and evolution.—As already stated, mendelian variation can arise by the recombination of the existing genes through hybridisation. Therefore fundamental change is provided for by the mutation. Mutations are not losses of genes but are only changes in genic structure. Mutations are mostly

recessive. Out of 300 mutations studied by Baur in *Antirrhinum majus* only 9 to 10 are dominant and the others proved to be recessive to the wild types. The direction and rate of mutation vary in different genes. Mutations with large effects cause large disturbances in the normal development and functioning. Therefore mutations with small effects are of importance in evolution. These are sometimes termed as *micromutations* and their effects sometimes are not readily observable. If these small variations prove to be of advantage to the organisms the latter have greater value in evolution. The accumulation of small changes, is in essential the principle of Darwinism *in a modified form. The hereditary variations by mutations are non-directive and non-purposive.* The mutations are not directed by the environment and also the mutations do not arise to fulfil any specified purpose for the organism. *Mutations arise and if they are useful to the organism they play their role in evolution.* The mutated genes work in harmony with the genotype of the organism in which they occur and is stabilised in the course of evolution. When such genes are transferred to new genotypic back-ground their behaviour is more complex, *e.g.*, crinkled dwarf in *G. barbadense* when transferred to *G. hirsutum* shows complex behaviour. When the new variations are subjected to geographic isolation there are chances for development of new species. By processes such as asexual reproduction, amphidiploidy, chromosome ring formation and intercross sterility, normal segregation is prevented genetically.

As examples for mutation providing chances for evolution of new forms, varieties or species, may be mentioned *Cicer gigas* and *Arachis hypogaea var. Gigantea.* The very popular improved strain in paddy G. E. B. 24 is suspected to have arisen by mutation in *Konamani.* Similarly, in ragi (*Eleusine Coracana*) E. C. 3735 arose by mutation in E. C. 593. The former is earlier in duration than the latter.

Chapter 10

POLYPLOIDY

POLYPLOIDS—INDUCTION OF POLYPLOIDY—COLCHICINE TREATMENT—CHANGES DUE TO POLYPLOIDY—AUTO-POLYPLOIDS—AUTO-TRIPLOID—AUTO-TETRAPLOID—ALLO-POLYPLOIDS—SECONDARY POLYPLOIDS—PENTAPLOIDS—HEXAPLOIDS—HAPLOIDS—POLYPLOIDY IN EVOLUTION—POLYPLOIDY IN BREEDING.

1. **Polyploids.**—A normal plant shows in each one of its body cell, twice the number of chromosomes found in the gametes. This doubling is due to the fertilisation effected by the union of male and female gametes with equal number of chromosomes. Such plants are termed diploids. Chromosomes are carriers of genes, and it has been pointed out in the preceding chapter that the genes are comparatively stable, but occasionally and fortuitously mutate. It was also pointed out that mutation includes changes in the structure of the chromosomes as well. There is yet another type of change which causes increase in the number of chromosomes in multiples of the haploid number and this is termed *polyploidy*. Thus, if n represents the haploid number of chromosomes then,

2n—diploid
3n—triploid
4n—tetraploid
5n—pentaploid
6n—hexaploid
7n—heptaploid
8n—octaploid
9n—nonaploid
10n—decaploid and so on (Fig. 59.)

A general survey of the chromosome numbers of various related species shows that the numbers form multiples of a *basic number*. The chromosome numbers of the plants in the family *Solanaceae* are listed below :

Atropa belladona	72
Capsicum annuum	24
C. annuum nigrum	12
Datura fastuosa	24
D. ferox	24
D. Metel	24
D. quercifolia	24
D. stramonium	24
Hyocyamus albus	36
H. Canadensis	72
H. niger	36
Nicotiana digluta	72

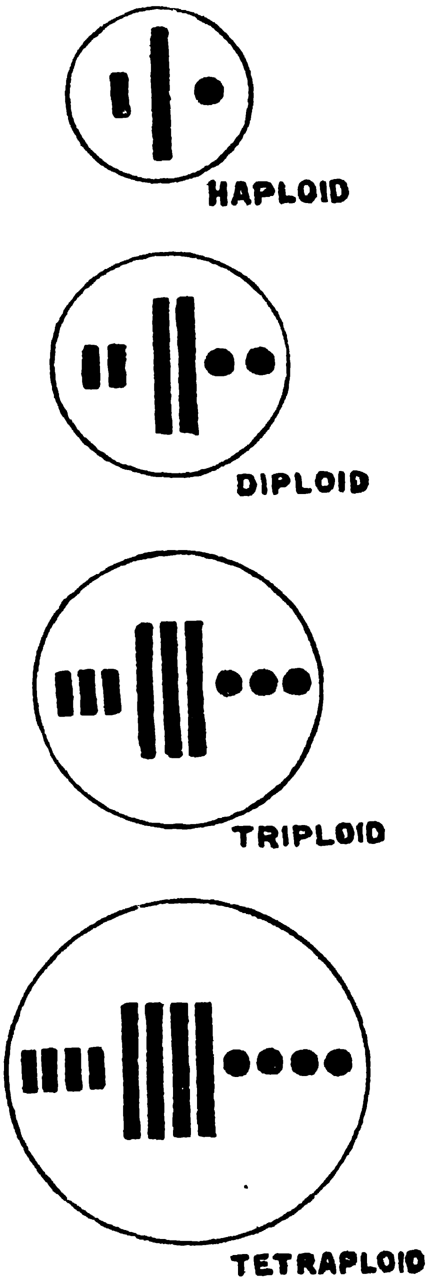


Fig. 59.—Diagram to illustrate polyploidy and the consequent increase in the chromosome complement of a cell.

N. rusbyi	24
N. sylvestris	24
N. Tabacum	48
Physalis peruviana	48
P. Philadelphica	24
Scopolia lurida	48

Solanum alatum	...	...	... 48
S. atropurpureum	...	...	... 48
S. marginatum	...	...	... 24
S. muricatum	...	...	... 24
S. nigrum	...	...	... 72
S. nigrum Var. gigas	...	...	... 144
S. tuberosum	...	...	... 48

The foregoing table shows that all the chromosome numbers listed out here fall into multiples of 12 which latter is termed basic number. Thus the species under *Solanum* are all multiples of 12. The different species constitute polyploids with 12 as the basic number.

The increase in chromosome number results by the doubling of chromosomes in a plant and it is termed *autopolyploid*; if the doubling results after a species has crossed with another it is termed as *allopolyploid*. In some cases, due to irregularities in cell division one or more unbalanced chromosomes become added to a diploid set of chromosomes. Such plants with extra unbalanced number of chromosomes are termed *polysomics*. These polysomics may form the basis for polyploidy and polyploids derived from them are termed *secondary polyploids*. Thus if (AA) represents the chromosome complement of a diploid species, (AAA) constitutes the chromosome complements of an autotriploid, (AAAA) that of auto-tetraploid and so on. If (BB) represents the chromosome complement of another species then (AAB) is an allotriploid, (AABB) is an allo-tetraploid and so on. (Fig. 60). In the autopolyploid (A) forms the basic number and in the allopolyploid (AB) forms the basic number. If (2A + 1), (2A + 2) etc., form the basic number of a polyploid series, then the latter are secondary polyploids.

A study of polyploids is important to the plant breeder because it offers scope to increase the chromatin content of a cell and thus bring about quantitative changes in the gene content which in turn may favourably affect the desirable characters in breeding material. This has varied consequences. Further, polyploidy has played a great part in the evolution of economic plants and a knowledge of the processes is helpful not only to reveal the relationship between different species, but is also of great significance in planning hybridisation for crop improvement.

2. Induction of Polyploidy.—It has been mentioned that aberrations in cell division may lead to polyploidy. Such irregularities in cell division may occur during mitosis or meiosis as indicated below.

Mitosis.—(*a*) Failure to form cell wall after the division of nucleus leads to doubling of chromosome numbers. If a shoot arises from such a cell, the former is tetraploid. If such a failure occurs in germinal tissue shortly before reduction division, diploid gametes are formed from such cells (syndiploidy).

(*b*) At anaphase, the spindle mechanism may fail to separate the sister chromatids to opposite poles. Consequently chromosome number is doubled.

Meiosis.—Polyploid gametes may result by aberrations during meiosis by (i) first, second or both the divisions may fail leading to the formation of *restitution nucleus* (ii) by the failure of mitotic division immediately preceding meiosis, P. M. C. with two or more nuclei are formed (iii) fusion of homotypic spindles may take place and (iv) double division of chromosomes during both the divisions of meiosis.

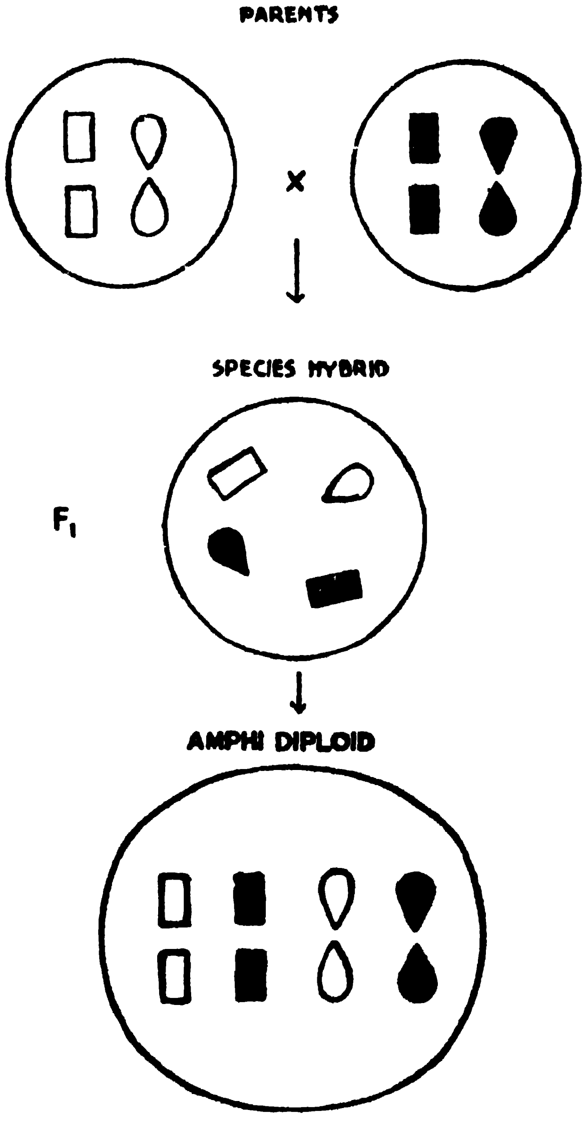


Fig. 60.—Amphidiploid. In the species hybrid, the paternal and maternal chromosomes lack homologues for pairing. When the chromosome number is doubled, the chromosomes pair regularly.

When plants are injured, the wounds are rapidly healed. In the course of rapid cell divisions to form callus and heal the wound, mis-steps in cell

division occur. In many cells, cell wall fails to form after cell division and this leads to doubling of chromosome number. When buds are formed from such tissues, polyploid shoots arise. Winkler (1916) noticed that about 7% of the buds formed from callus tissues developed into polyploid shoots.

Since polyploidy was noticed to alter many characteristics of the plant, attempts were made to artificially induce polyploids. Nebel and Ruttle (1938) working on *Tradescantia, Petunia,* Snap-dragons and marigolds and Blakeslee and Avery (1937) working on *Portulaca, Datura and Cucurbita* noticed that the alkaloid colchicine was very effective in doubling the chromosome number. This alkaloid is extracted from the plant (*Colchicum autumnale* (*Liliaceae*) which is found in the temperate region around the Mediterranean and Central Asia. *C. luteum* is an allied species found in the Western Himalayas. This alkaloid is widely used by various workers and is found applicable in its desired effect in various types of plants.

Gloriosa superba L. (Liliaceae) is reported by Parthasarathy (1941) to contain the alkaloid colchicine. The extract from the tubers of this plant showed positive results when maize seed was treated.

Whitkus and Berger (1944) have reported another chemical, Veratrine sulphate which is similar to colchicine in its effects on cell division. It is a

[*With the kind permission of India Govt. from Ind. Fmg.*].

Fig. 61. Application of colchicine to a vegetative bud.

mixture of alkaloids, chiefly veratrine and cevadine with small amounts of two others. This was first successfully tried on onion root tips.

Cytological effects of treatment with *veratrine* are the same as in colchicine with few differences. In the former, the division of spindle attachment region is delayed. In many cases partially functional spindle may be formed and incipient anaphase and even telophase may be evidenced, but in no case cell wall is formed. The final effect may be brought about in any one of the following three ways :

(1) complete failure of spindle formation.

(2) Fusion of nuclei after pseudo-anaphase.

(3) Formation of sticky chromosome bridges.

Reports from Russian work show that the chemical 'Granosan' is as effective as colchicine.

3. **Colchicine treatment.**—The technique for the application of colchicine in the various plants may be summarised as follows :

(1) Twigs may be immersed in solutions of varying concentration and the immersion tried for varying duration.

(2) Solutions of colchicine in agar may be applied to growing buds when the solution is warm and in liquid state. In such applications the concentration required is much higher than in aqueous solutions.

[*With the kind permission of India Govt. from Ind. Fmg.*]

Fig. 62. Application of colchicine to germinated seeds.

(3) The colchicine solution may be allowed to reach the growing bud through a capillary string.

(4) The colchicine solution may be allowed to drop on the growing bud at proper intervals (Fig. 61).

(5) The solution may be sprayed on the growing region. The spraying must be done at intervals.

(6) The chemical may be applied as a paste in lanolin.

(7) The best results are generally obtained by using seeds. These are soaked in the aqueous solution of colchicine. The seeds may be subjected to pre-soaking in water for 24 hours and then immersed in colchicine solution. (Fig. 62). Varying strengths of solution and periods of immersion are to be tried for different plants.

(Photo from Cotton Specialist).

Fig. 63. Vegetative Shoots from (*G. anomalum* × K_1) F_1 hybrid and the amphidiploid from the same.

The general symptoms indicating the effective action of the chemical are :

(1) Immediate effect is arrest of growth.

(2) Leaves and flowers are bigger ; the hairs on them are thicker and coarser.

(3) Stomata are bigger in size.

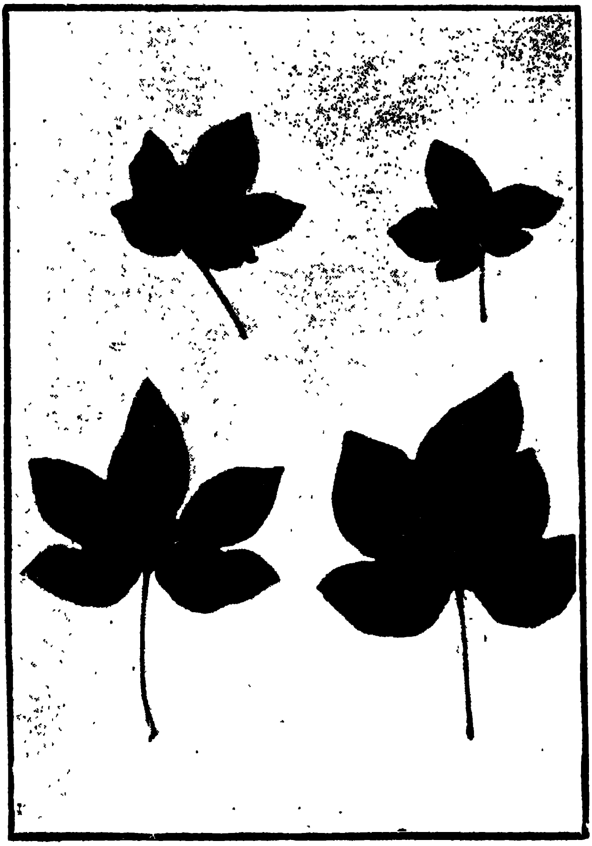
(4) In seed treatment, the cotyledonary node is bigger.

(5) Flowering is delayed.

(6) If the application is to a sterile hybrid, fertility is restored. In the case of autopolyploids, sterility to a smaller or larger percentage is evident.

Colchicine brings about doubling by acting on the spindle mechanism. During mitosis, the chromosomes appear longitudinally split even from prophase and the two chromatids separate to the two poles at anaphase. Colchicine acts on the spindle mechanism and the separation of the split chromosomes

is thus arrested. Instead of forming two daughter nuclei, a single nucleus with double the number of chromosomes is formed.



(*Photo from Cotton Specialist*).

Fig. 64. Leaves from (top left): K_1 (top right): *G. anomalum*. (Bottom left): Species hybrid *G. anomalum* K_1 ; (bottom right): F_1 doubled amphidiploid.

In applying this chemical various techniques are adopted. Details in respect of few crops where colchicine was applied are discussed (Fig. 65).

(*i*) *Cotton*.—Colchicine was used in doubling the chromosome number in the partially fertile hybrid of the cross *Gossypium anomalum* (2n—26) × *G. arboreum var. neglectum forma indica* (2n—26) (Karunganni cotton). (Figs. 63, 64). Shoot tip of young plant bearing 4—5 leaves was wetted with 0.08% aqueous solution of colchicine at intervals for a period of 12 hours and subsequently washed with distilled water.

The effects of the treatment were : leaves were larger, darker in colour, leathery in texture, leaf lobes overlapped and twisted; stomata, bracts, pollen grains bolls and seeds in the treated plants were bigger than in the control ; the treated plants were late maturing, lint coloured, ginning percentage poor and the plant more fertile in comparison to the control. The resulting plant with 2n—52, crosses with both K1 and the New World cultivated cottons.

(ii) *Bengal gram* (*Cicer arietinum*).—The following technique was adopted. Seeds were soaked in water for 24 hours and placed on moist filter paper. When radicles were just emerging, the seeds were immersed in aqueous solution of colchicine of different concentrations—0.25%, 0.5% and 1.0% and for periods ½ hour 2 hours 6 hours and 24 hours. In none of the treatments all the seeds were equally affected. Increased concentration and duration of the treatment showed more pronounced effects and after a certain limit the treatment completely checked growth and the seedlings died out. (Table 35). Fig. 65 shows six days old seedlings from treated seeds.

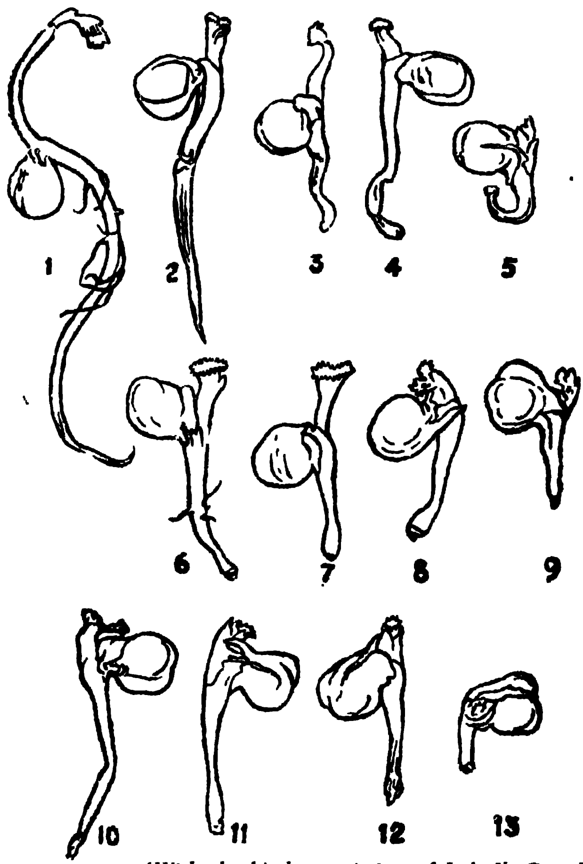


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Fig. 65. 1. Untreated; 2, 3, 4, 5: Treated with 0. 26% colchicine for ½, 2, 6 and 24 hours respectively. 6, 7, 8, 9: Treated with 0. 5% colchicine for ½, 2, 6 and 24 hours respectively. 10, 11, 12, 13: Treated with 1% colchicine for ½, 2, 6 and 24 hours respectively.

Treatment of seeds with 0.25% solution for ½ hour appears to be the best. Out of 26 treated plants, only 13 showed the effects of the treatment and the other 13 developed like untreated controls. The immediate effect of treatment was swelling of radicles and retardation of their growth. The seedlings from effectively treated seeds showed slow growth with thicker stems and darker and broader leaves. They flowered 4–5 days later than the controls. Sizes of pollen and guard cells are bigger in the treated plants. Pollen

TABLE 35.

—	0·25%					0·5%					1·0%					Control.		
Duration of Treatment.	No. of seeds treated.	No. of plants obtained.	No. of polyploids.	% Survival.	% Polyploids.	No. of seeds treated.	No. of plants obtained.	No. of polyploids.	% Survival.	% Polyploids.	No. of seeds treated.	No. of plants obtained.	No. of polyploids.	% Survival.	% Polyploids.	No. of seeds.	No. of plants obtained.	% Survival.
½ hour ...	10	10	6	100	60	10	4	1	40	10	10	3	1	30	10	10	10	100
2 hours	10	4	1	40	10	10	2	1	20	10	10	...	...	...	...	10	10	100
6 „	10	3	3	30	30	10	...	...	...	...	10	...	...	...	...	10	10	100
24 „	10	...	...	...	...	10	...	...	...	...	10	...	...	...	...	10	10	100

sterility varied from 40 to 80 per cent as compared to 10 per cent in the controls. Cytological examination of the progenies from these 13 plants yield the information summarised in table 36.

TABLE 36.

Plant No. in 1938–'39.	No. of seeds sown.	No. of plants obtained.	No. of diploids $2n=16$.	No. of Polyploids $2n=32$.	Remarks.
5	11	6	2	4	1 branch mixoploid.
7	7	7	2	5	Do.
9	2	2	...	2	
10	35	29	28	1	1 branch mixoploid.
31	6	6	6	...	Do.
23	2	1	...	1	
31	4	3	...	3	...
61	4	2	1	1	1 branch mixoploid.
62	11	11	9	2	Do.
63	1	1	...	1	...
8	5	4	4	...	Doubtfully mixoploid.
2	Did not germinate.				
44	Did not germinate.				

The 13 plants from treated seeds were not uniform in all their branches ; some branches were diploids and some others tetraploids.

(*iii*) *Chilli* (*Capsicum annuum*).—Seeds were immersed in 0.05%, 0.1%, 0.2% and 0.4% solution of colchicine for 1, 2, 4, 6 and 8 days. Immediate effects of treatment were : roughening and thickening of leaves, fasciation of stems and other vegetative organs and doubling of flowers ; the plant was slow growing with broad and succulent leaves and flowered later : the pollen grains were double in size and showed varying percentage of sterile pollen. The effect of treatment in producing polyploids is shown in the following table 37.

TABLE 37.

Period of immersion.	Colchicine solution.			
	0·05%	0·1%	0·2%	0·4%
1 day ...	6·9	4·8	73·3	60·0
2 days ...	17·4	13·0	68·8	71·4
4 „ ...	37·5	28·6	80·0	...
6 „ ...	15·8	33·3	50·0	50·0
8 „ ...	30·8	60·0	12·5	3

Besides tetraploids, a triploid, a mutant (Fig. 66) and diploids, with meiotic irregularities were also noticed in the treated plants. There were also periclinal chimeras with 4n epidermis over 2n tissues. In the second generation

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Fig. 66. A mutant in chilly.

after the treatment, progenies of first generation tetraploids were either all tetraploids or some tetraploids and some diploids. The latter indicate that some of the first generation tetraploids were mixoploids.

(*iv*) *Gingelly* (*Sesamum orientale*).—The following three methods were tried in the use of colchicine with this crop.

(1) Seeds were immersed in colchicine solutions for different periods.

(2) Seeds were germinated on blotting papers soaked in different concentrations of colchicine solution.

(3) Young flower buds were immersed in test tubes filled with different concentrations of colchicine and the immersion lasted for varying periods.

In all cases, the materials were washed with distilled water. 7 abnormal plants were noted out of 100 seeds treated as mentioned in treatment (1) with 0·06% solution for 2 hours. The immediate effects of the treatment were swollen hypocotyl, thick cotyledons, stunted roots, broad, coarse and thick leaves.

Sesamum orientale (n—13) was crossed with *S. prostratum* (n—16). The hybrid was intermediate in respect of many characters. It flowered profusely but set no seeds and cytological study revealed 29 as the somatic chromosome number. 0·4 per cent colchicine was sprayed on the vegetative buds of the

hybrid twice daily on three alternate days. The treated buds showed symptoms of induced polyploidy and these latter were highly female fertile though pollen fertility was not equally good.

(v) *Tobacco.*—The following methods were adopted in the case of hybrid *Nicotiana glauca* × *N. plumbaginifolia*

(1) Vegetative buds were immersed in 0·5% and 0·25% aqueous solution of colchicine for 24, 48 and 72 hours respectively in each case.

(2) Colchicine was applied as a paste in anhydrous lanolin with 0·4% strength. Growing vegetative buds were treated.

(3) Growing buds were wetted with 0·4% aqueous solution twice daily at 11 A.M. and 3 P.M. for 10–15 minutes each time for a week.

The third treatment only was successful and the first two proved to be drastic in effect.

The following symptoms of effect were noticed; unequal growth and thickening of leaves, increased size of stomata, fasciation in leaves and flowers; this plant proved to be a chimera as the pollen grains proved to be normal.

Different concentrations of colchicine with glycerine or alcohol added in varying proportions to facilitate penetration of the tissue by the drug gave chimeras only.

4. Change due to Polyploidy.—The change brought about by doubling of chromosomes has far reaching effects both on the individual and in evolution of species. *Morphological, physiological and genetical changes follow such chromosomes doubling. The stem of polyploid is stouter and thicker, leaves are larger, broader and thicker and darker green, hairs on vegetative parts are coarser and thicker, and the floral parts, fruits and seeds are bigger than in diploids. In general the polyploid forms exhibit gigas character.* This is probably due to the cells being larger in size which is necessitated by the increase in chromosome number. This gigas character is not only exhibited by the artificially induced polyploids but also by the naturally existing ones.

The differences are noticeable in physiology and reaction norms. Becker (1931) states that osmotic concentration in autopolyploids is proportional to chromosome number. In maize autotetraploid, it takes longer time for the grain to mature. In fruits and vegetables vitamin content is increased. In corn meal the tetraploid form contains 40% more vitamin than the diploid. In tobacco nicotine content increases and also total nitrogen, calcium, potassium and magnesium but there is decrease in carbohydrate, sulphur and phosphorus. In triploid beet, sugar content increased. In cucurbita the shape of the fruit changes due to polyploidy.

The following data (table 38) provide a comparative statement in respect of tetraploid in Bengal-gram induced by colchicine treatment.

TABLE 38.

Character.	Tetraploid.	Diploid.
Pollen size	43·75 to 46·87 μ	34·375 μ to 37·500 μ
Pollen sterility range	40% to 80%	nil to 5%
Number of main branches	8·38 ± 0·68	10·8 ± 0·47
Number of leaves on tallest branch	25·85 ± 0·37	25·54 ± 0·24
Height of plant in cm.	30·26 ± 0·72	29·49 ± 0·41
Number of leaflets per leaf	14·03 ± 0·13	13·74 ± 0·03
Length of leaflet in cm.	1·027 ± 0·025	0·92 ± 0·01
Breadth of leaflet in cm.	0·6452 ± 0·014	0·4483 ± 0·004
Length of guard cell of stomata	30·97 ± 0·1257	24·21 ± 0·09665
Maximum length of flower standard in cm.	1·106 ± 0·1442	0·911 ± 0·0079
Maximum breadth of flower standard in cm.	0·9194 ± 0·0144	0·6946 ± 0,072
Number of days from sowing to flowering.	65·3	62·4

In general the range of variability is greater in tetraploid than in the diploid form. Similar data in respect of an allopolyploid are furnished below.

An African wild cotton *G. anomalum* (n—13) was crossed with K1 an improved strain in *G. arboreum var. neglectum forma indica* (n—13). The hybrid was partially sterile. The hybrid plant was treated with colchicine and the resultant polyploid showed darker leaves more leathery in texture than the hybrid and the treated plant grew to a height of 12 feet before it flowered. Data of measurements relating to the parents, hybrid and the amphidiploid are given in table 39.

Polyploidy thus leads to new physiological properties and this in turn leads to the formation of new kind of organisms which proceed in new lines in regard to variation and mutation. Though cell size increases in them, growth rate is decreased and thus even in artificially induced polyploids the flowering is delayed. *This decreased growth rate slowly leads to the formation of perennial types from annual types.* Thus Sharp (1934) reports that autotetraploid *Zea* race is perennial while the diploid is annual. This has been amply confirmed by a study of the chromosome number in perennial and annual species and also by a comparison of the forms with the artificially induced polyploid forms. Thus Longley (1924, 1932) states that of the two species of *Euchlaena*, *E. mexicana* is a diploid and annual and *E. perennis* is autotetraploid and a perennial. Similarly *Sorghum sudanense* and *Sorghum halepense* are hardly distinguishable except that the former is annual (n—10) and the latter perennial (n—20). *S. versicolor* (n—5) is a short lived annual with a more shortened span of life than the other species. Muntzing (1936) collected data to show the striking relationship between chromosome number and life form of plants. He concluded that a large number of perennial species must have originated from annual types with lower chromosome number.

Polyploidy leads to deviation in genetic behaviour as compared to the diploid forms. In a normal diploid two allelomorphic genes are present but

TABLE 39.

Character.	G. anomalum.	G. arboreum. (K1).	G. anomalum × K1 untreated F1.	G. anomalum × K1—treated F1.	Remarks.
1. Leaf index	1·32	1·25	1·45	1·16	Main leaves on monopodial branches
2. Length of guard cells of stomata of leaves in μ .	21·5	25·6	28·1	36·1	From lower epidermis on mature leaves.
3. Bract { Length in mm.	15·8	28·4	36·2	46·3	} Measured on the day of flowering.
Breadth in mm.	5·3	29·9	22·6	30·1	
4. Petals { Length in mm.	37·6	36·6	42·9	53·0	} Do.
Breadth in mm.	37·1	30·5	43·0	49·6	
5. Pollen grain diameter in μ (air medium) ...	102·1	103·3	94·5	128·5	From fresh flowers between 10—11 A.M.
6. % of shrivelled pollen	3·0	8·7	73·3	33·8	
7. Boll { Length in mm.	24·7	28·0	21·6	34·8	} Measurement from 4 locked bolls.
Breadth in mm.	14·0	22·3	13·7	23·6	
8. Weight of 100 seeds in decigrams	19	51	40	70	
9. Weight of lint for 100 seeds in decigrams ..	2	21	11	19	
10. Lint length in mm., ...	6·2	26·2	23·0	26·2	Halo length
11. Seed size	Small with short *fuzz.*	Medium with very short *fuzz.*	Medium with medium *fuzz.*	Big with long *fuzz.*	
12. Diameter of the fibre in μ	...	22·0	..	18·9	
13. Fibre weight	..	1·85		1·22	

in polyploid forms more than two are present. When a gene mutates in a polyploid *e.g.*, in a triploid AAA the genotype may change to AAA' where A' represents the mutated gene. The chances for A' to express itself in phenotypes are much less than in diploids and this is a relieving feature in such cases where the mutant form is deleterious or uneconomic. Even in cases where the mutation is in a progressive direction, the plant has still the normal genes left over to carry on the normal function, while the mutated gene will add to the selection value without altering the existing character. *Thus, the polyploids have a reserve of genes—the surplus number over the diploid—which may mutate in different directions.* If deleterious, their effects are minimised ; if advantageous they lead to the development of better types.

In tetraploid forms there are four homologous chromosomes and in heterozygous condition there are two of each kind. On segregating in F_2, the duplicate genes cause 15 : 1 ratio in the place of 3 : 1 in a normal diploid. Therefore, as already pointed out presence of a large number of duplicate genes in a plant, suggests that it is an autopolyploid of comparatively recent origin. In all such cases, the rate of mutation is much smaller as compared to the diploid allies. Stadler reports it to be so in maize. Similarly, ragi has so far shown very few mutations as compared to the other cereals and in this crop a large number of characters is governed by duplicate factors.

5. **Autopolyploids.**—Presence of more than two sets of chromosomes in autopolyploids results in complex meiosis. It was pointed out in Chapter V that during meiosis similar chromosomes pair and crossing over takes place between them. When there are more than two homologous chromosomes, three in triploids, four in tetraploids and so on, the pairing is more complex. At any one point two chromosomes only can pair. In autopolyploids, homologous complements come together ; at any one point pairing is between two chromosomes only. It may happen as in triploids, that two chromosomes only may pair leaving the third unpaired. Pairing between chromosomes of the same parental origin is termed *autosyndesis*. In autopolyploids pairing is strictly autosyndetic. Multivalents appear at heterotypic metaphase and the separation of chromosomes is not generally half and half as in diploids. Unequal separation of chromosomes may result in reduced cells with more than 2n or less than 2n chromosomes.

Multivalency at metaphase interferes with normal *disjunction* or separation of chromosomes at anaphase. Due to this *non-disjunction* two types of abnormalities occur in the gametes. Due to such abnormalities in meiosis there is certain amount of sterility in autopolyploids.

6. **Auto-triploids.**—Autotriploids have been noted in a number of crop plants. Triploidy was first reported by Gates (1908) in *Oenothera*. Ramiah *et al* (1933) isolated autotriploid in a pure line rice, and Rangaswamy Iyengar *et al* (1942) have reported it in pearl millet. Ichi Juma noted a triploid in X-rayed paddy seed. Pal *et al* (1942) reported it in chilli when the seeds were treated with Colchicine. Triploids may arise by any of the following ways. (1) *By failure of reduction, in mega-sporogenesis diploid gametes are formed, which on fertilisation by haploid pollen give rise to triploid zygotes.* (2) *By somatic doubling taking place in germ tract, cells with 4n chromosomes undergo reduction division and give rise to diploid gametes which on fertilisation by haploid gametes form triploids.* (3) *When tetraploids cross with diploids, triploid progenies arise* (4) *Haploid egg may be fertilised twice by two haploid male gametes when the triploid progenies result. This type of fertilisation is termed dispermy.*

In plants, nucellar embryony gives rise to diploid eggs and the fusion of P. M. C. gives rise to diploid pollen. In most cases triploid plants arise by fertilisation of diploid egg gamete by haploid pollen and it is generally believed that diploid eggs are more functional than diploid pollen.

Cytological behaviour of auto-triploid in rice is briefly discussed below.

Mitosis.—No irregularities are noticed in somatic divisions. In prophase, three chromosomes are attached to the nucleolus instead of two of diploids. At early telophase three nucleoli were formed. The volume of nucleolus in the triploid showed no increase over that of diploid.

Meiosis.—In a few cells at diakinesis 12 trivalents are noticed. In majority of cells, trivalents, bivalents and univalents in varying proportions are found. Trivalents assume rod, pan, Y and triple shapes of which the pan type is the most common. At metaphase I, trivalents and bivalents lie haphazard on equatorial plate and the univalents lie outside the spindle. In the case of bivalents the disjunction is normal while the trivalents separate at two to one pole and the third to the other pole causing numerical difference in chromosome number of the daughter cells. The lagging univalents split and the split halves may go to the same pole or may be extruded and lost in cytoplasm. Rarely they constitute a micronucleus in the daughter cell. Second division is more regular with fewer laggards. The divided univalent of first division do not divide again but are unequally distributed to the two poles. Any lagging univalent may be left out of the daughter nucleus. Irregularity by way of random distribution of chromosomes throughout the spindle may be present in second division. Division of *dyads* is generally simultaneous, but delay in any one of them may cause formation of *triads* instead of tetrads. By non-disjunction of trivalents in first division unreduced gametes may be formed (Fig. 67).

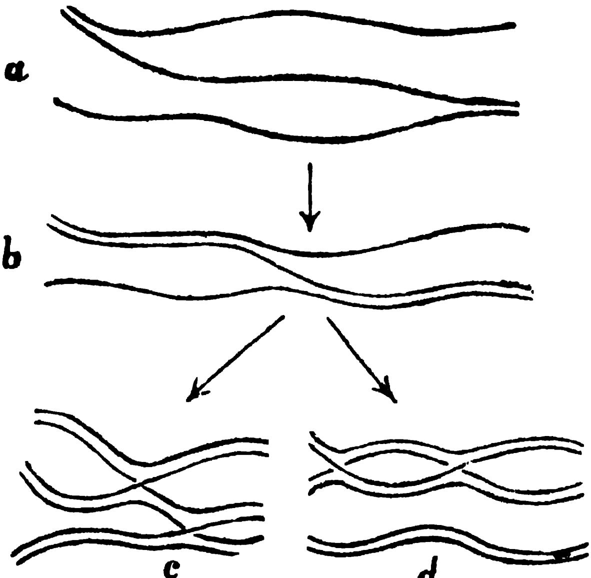
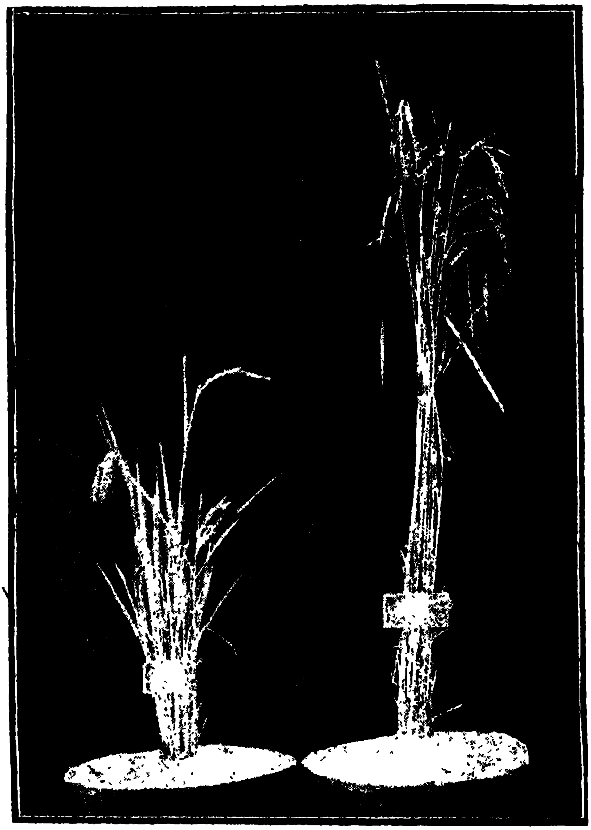


Fig. 67. To illustrate the structure of pairing chromosomes during prophase of first division in Triploids, a: Zygotene ; b : Pachytene ; c & d : diplotene

(after Darlington)

Due to abnormalities in meiotic cell division functional gametes are rarely formed in triploids. They are mostly sterile and rarely set seed on selfing or out-crossing. In the rice triploid described above, 150 fully developed grains set by natural crossing out of a total of 410,000 spikelets, or roughly the setting is 0·037%. Anthers do not dehisce due to malformation of pollen grains The progenies of triploids showed varying somatic numbers 24 to 30. The progenies with more than 24 chromosomes are *aneuploids*. This results because of the fact that during meiosis, out of three sets in each chromosome, two disjoin normally to the two poles and the third behaves irregularly causing gametes with more than n number of chromosomes. This increased number may be anything from 1 to 12 in rice where the haploid number is 12. The resulting gametes on fertilisation by a normal haploid gamete will show (2n + 1), (2n + 2), (2n + 3) etc., where the additional chromosomes may be any one of the haploid complement. Fig. 68 shows a *trisomic* rice plant i.e., plant with 25 somatic chromosomes. However all the theoretical combinations are not met with because of the fact that with increase in the odd number of chromosome, the gametes become non-functional and with increase in such chromosome numbers, the plants become less vigorous. The limiting factors for obtaining plants with binomial distribution of extra chromosome, are (1) failure of seeds to germinate or the death of seedlings in their very early stages, (2) failure to form good seeds due to the unbalanced condition of the chromosomes in the zygote. It is also noticed that the gametes fail to function normally when their chromosome number increases beyond a certain limit over the haploid complement. After this limit, the gametes

with 2n chromosome number only function. Thus, for example, in the case of rice, plants with 2n –29 are developed but the next higher number is the triploid with 36 chromosomes.



(Photo from Paddy Specialist).

Fig. 68. Trisomic and diploid plants in rice.

Triploids were reported in *Pennisetum typhoides* (Fig. 70) and *Brassica campestris*.

7. **Auto-tetraploid.**—A plant with four sets of homologous chromosomes is termed a tetraploid. Tetraploids may arise by somatic doubling when tetraploid branches are formed, especially from buds initiated by callus tissues. Somatic doubling generally happens by the failure of first mitotic division in the zygote. This may also arise by diploid gametes coming together but the chances for a diploid gamete to meet a haploid gamete are greater than for two diploids. *Tetraploids exhibit gigas character and show partial sterility. The progenies are generally tetraploids.* When crossed with diploids they give rise to triploids.

In wild paddy *Oryza longistaminata*, an auto-tetraploid was isolated (Figs. 69, 71). This arose by somatic doubling. A clump with thicker stem, darker pigments on internodes, broader, darker and thicker leaves and larger spikelets was noticed. The pollen grains were bigger in size with higher abor-

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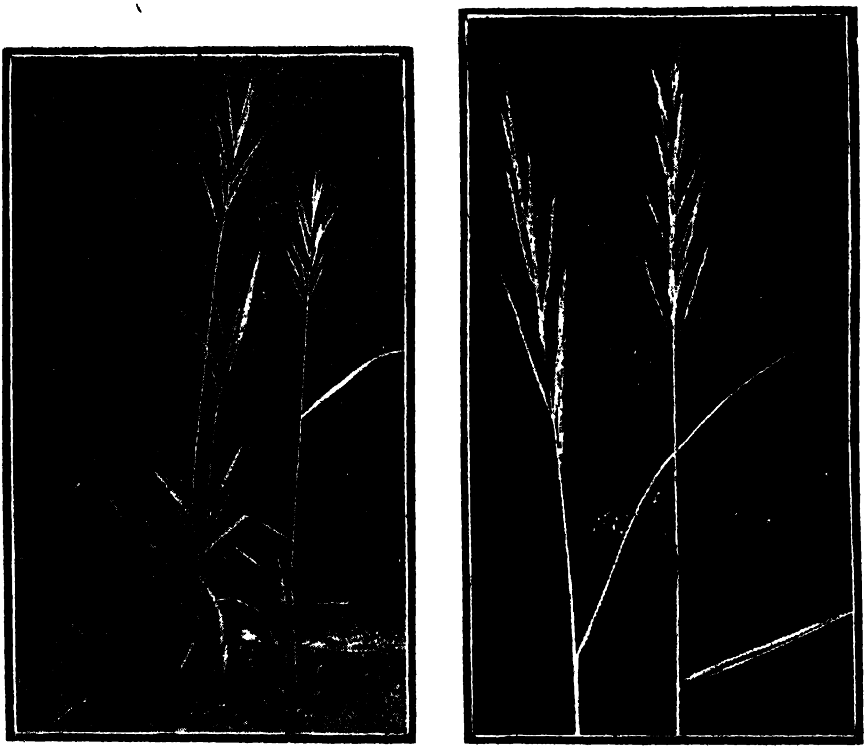
Fig. 70. Meiosis in Triploid pearl millet a, b, c : Diakinesis ; note the Y shaped and ring chromosomes. d. late diplotene ; *e, f, g, h* : pairing of nucleolar chromosomes ; *i*. interlocking *j* : late diplotene abnormal pairing ; *k* : diakinesis showing no trivalents.

tion. Cytological observations in somatic cells revealed 48 chromosomes instead of 24 of a diploid. At diakinesis, chromosomes were largely found in tetravalent groups in the form of rings, rods X and S although bivalents and rarely univalents were also present. At anaphase, lagging chromosomes and delayed splitting of univalents were also noticed. As a result of irregular reduction division, the distribution of chromosomes to the two poles is varied

(*Photo from Paddy Specialist*).
Fig. 69. Tetraploid in rice.

and daughter cells with unequal number of chromosomes arise.



(*Photo from Paddy Specialist*).
Fig. 71. Diploid and tetraploid plants in wild rice, *Oryza longistaminata*. On the right are earheads from the same.

In chilli (*Capsicum annuum*), auto-tetraploids were artificially produced by treating the normal diploid with colchicine (Fig. 72). The tetraploids showed bigger pollen grains, fruits, seeds and guard cells (Fig. 73, 74 and 75) and 48 chromosomes at metaphase I as against 24 of a normal diploid. Varying numbers of quadrivalents, trivalents, bivalents and univalents were met with (Fig. 76).

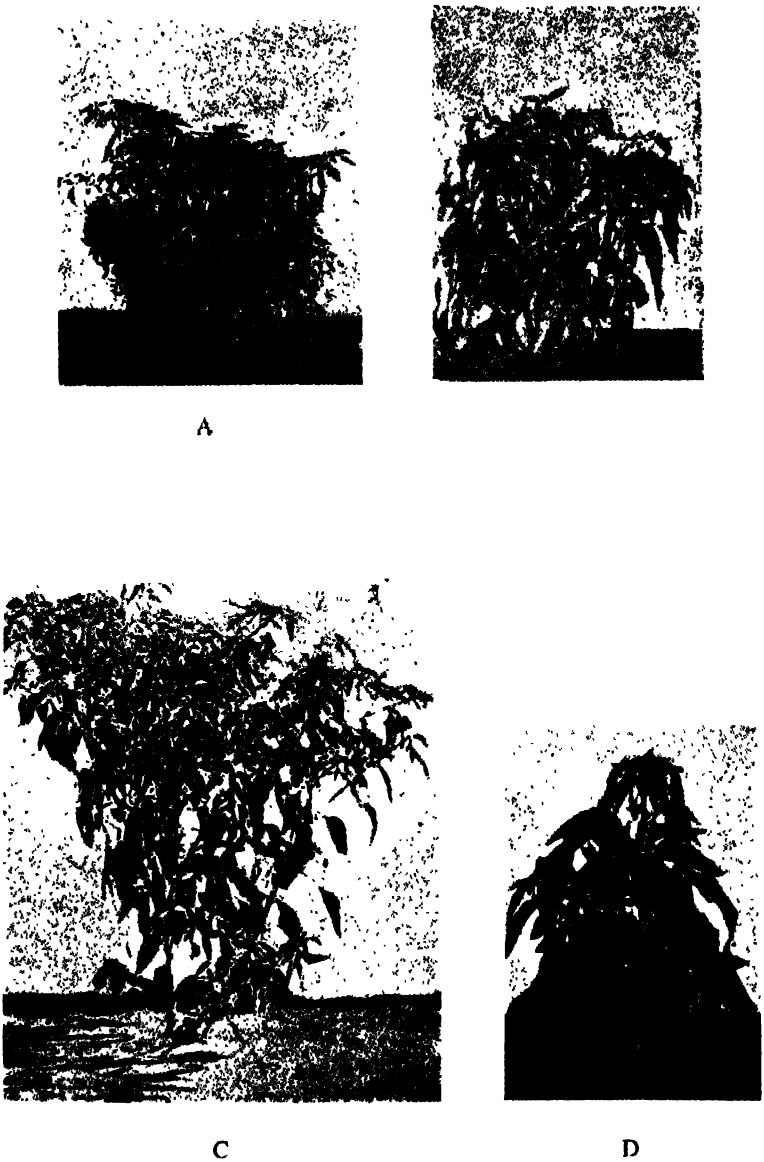
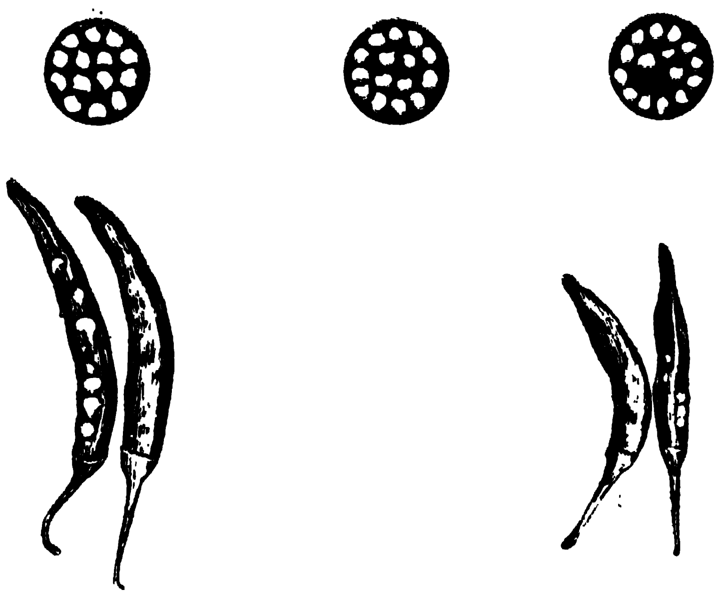


Fig. 72. Tetraploid chillies *Capsicum annuum*. A : Diploid ; B, C and D : Tetraploids Note the variation between the tetraploids.

(*With the kind permission of Ind. Jl. Gen. and Pl. Br.*).

Fig. 73 Pollen grains from diploid and tetraploid chilly. Note that the tetraploid pollen grains are large in size and there are a large number of ill developed grains.
(*With the kind permission of Ind. Jl. Gen. and Pl. Br.*)



(*With the kind permission of Ind. Jl. Gen. and Pl. Br.*).

Fig. 74. To illustrate the size of fruits and seeds in triploid, diploid and tetraploid chillies, *Capsicum annuum*,

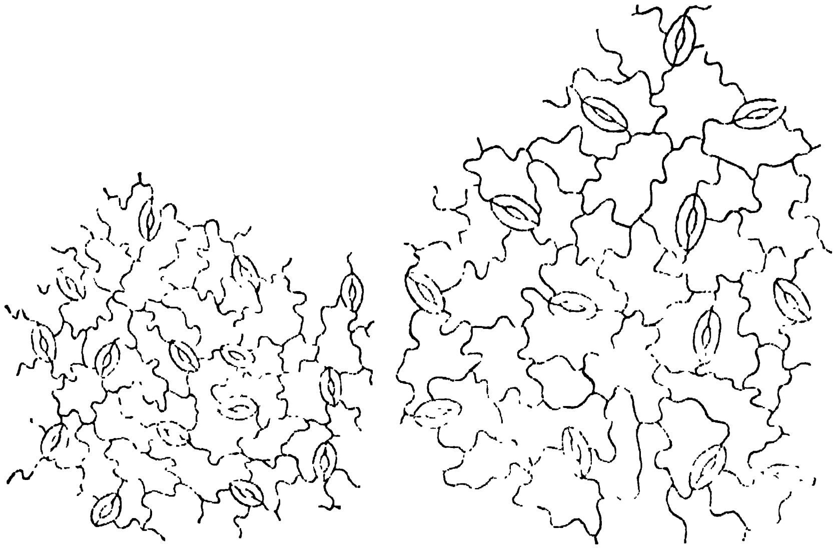


Fig. 75. Stomata in diploid and tetraploid chilly. Note the larger size of epidermal cells and stomata in tetraploid.
(*With the kind permission of Ind. Jl. Gen. and Pl. Br.*).

The following table shows the frequency of quadrivalents met with in the autotetraploid chilli.

TABLE 40

Number of quadrivalents per cell.	0	1	2	3	4	5	6	7
Frequency	11	34	53	48	69	28	3	2

Among 51 cells examined, 31 showed distribution of 24—24 chromosomes, 19 cells showed 25—23 distribution, and one cell showed 26—22 distribution. Tetrads were most commonly met with though dyads and triads were also met with. Therefore, formation of multivalents in metaphase I leads to certain amount of sterility in auto-tetraploids.

In Gossypium arboreum and G. herbaceum auto-tetraploids (2n—52) were artificially produced. These did not set bolls. They proved to be pollen sterile. They do not cross with the cultivated Asiatic cottons, but cross with the American types (2n—52).

The genetic behaviour and consequently segregation of factors and F_2 ratios in a cross are somewhat different. This has been worked out in *Datura*.

Purple tetraploid	PPPP
X	
White tetraploid	pppp
F_1 : Purple	PPpp

Gametes of F_1 : 1 PP, 4 Pp, 1 pp (6 types).

On selfing the F_1 there are 36 gametic combinations of which 35 are purple and 1 white. Back-crossing with the recessive parent will give a ratio of 5 : 1.

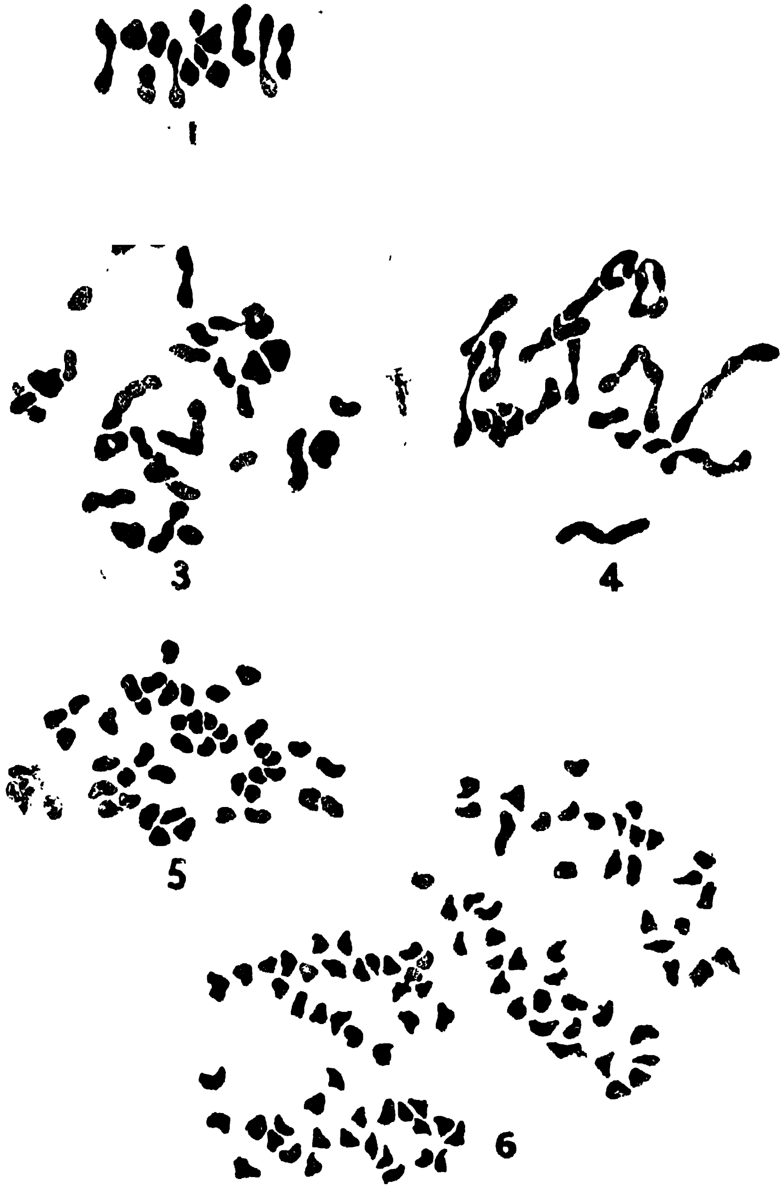


Fig. 76. Meiosis in tetraploid chilly. (1) Diploid : shows 12 bivalents in metaphase. (3) & (4) Diakine in the tetraploid showing associations of 4 chromosomes. (5) Anaphase I. (6) Anaphase II in a tetraploid.

(*With the kind permission of Ind. Jl. Gen. and Pl. Br.*).

Segregation of characters in tetraploids depends upon the types of pairing between the chromosomes—*viz.*, auto—or allosyndesis.

Cytology and genetics of the following tetraploids have been studied in *Primula sinensis*, *Datura stramonium* and *Lycopersicum esculentum*. Due to the formation of quadrivalents in meiosis, gametes with more or less than $2n$ number of chromosomes may be formed. The pairing chromosomes do not regularly disjoin and pass to opposite poles as in normal diploids. Non-disjunction at anaphase affects the genic constitution of the gametes. The gametes may possess different number of chromosomes, or, when they possess $2n$ number, some parts of chromosomes which paired may go to the same gamete. Both these have direct effect on the inheritance of characters in the tetraploids.

8. **Allopolyploids.**—In a preceding chapter it was pointed out that during meiosis homologous chromosomes are mutually attracted and that they pair. In diploid organisms, there are homologous pairs of chromosomes. During meiosis the chromosomes group themselves in pairs, *i.e.*, they form bivalents. In the preceding sections of this chapter it has been pointed out that autopolyploidy makes it possible for more than two chromosomes to be homologous, *e.g.*, *in auto-tetraploid there are four homologous chromosomes. In such cases during meiosis more than two of the homologous chromosomes are mutually attracted*, i.e., *multivalents are formed.* When a pure diploid species is crossed with another diploid species, in the cells of the hybrid there is one haploid complement from each of the parental forms. Since the parental species differ widely from each other, the two haploid complements of chromosomes in the hybrid are different. Therefore any one chromosome from the parental species finds no homologue in the maternal complement. *Consequently, during meiosis in such species-hybrids, the chromosomes lie about as univalents. Separation to the poles at anaphase is irregular and the resulting gametes are non-functional with the net result the hybrid is sterile. The sterility is caused by non-homology between chromosomes and non-pairing between them during meiosis. If the chromosome number in such a hybrid is doubled, each chromosome is duplicated. Pairing between the duplicated chromosomes is perfect, meiosis is fairly regular and fertility is restored.* Such a hybrid in which the chromosome number is doubled is termed *allotetraploid* or *amphidiploid*. Thus if AB represents a cross, then the amphidiploid is represented by AABB. The pairing of A with B depends upon the degree of homology between A and B. If they are not closely related, pairing is strictly between A and A. This is *autosyndesis* and if A pairs with B, it is *allosyndesis*. In the case of autosyndesis strictly bivalents only appear while in allosyndesis tetravalents are formed. By the type of pairing the degree of homology can be judged.

It has been pointed out that auto-tetraploidy increases sterility due to irregular meiosis, mainly by non-disjunction of multivalents. In the case of species crosses, the F_1 is generally highly sterile. This is due to non-pairing between the dissimilar sets of chromosomes contributed by the two parents. This sterility is overcome by doubling the chromosome complements.

Raphanobrassica is an example of experimental production of new forms by doubling chromosome complements in species hybrids. Karpechenko artificially produced this new type in 1927. Radish (*Raphanus sativus* 2n = 18) was crossed with cabbage (*Brassica oleracea* 2n = 18). The hybrid showed 18 chromosomes of which 9 were from radish and 9 from cabbage. The F_1 hybrid was sterile. At meiosis, the chromosomes did not pair and they were

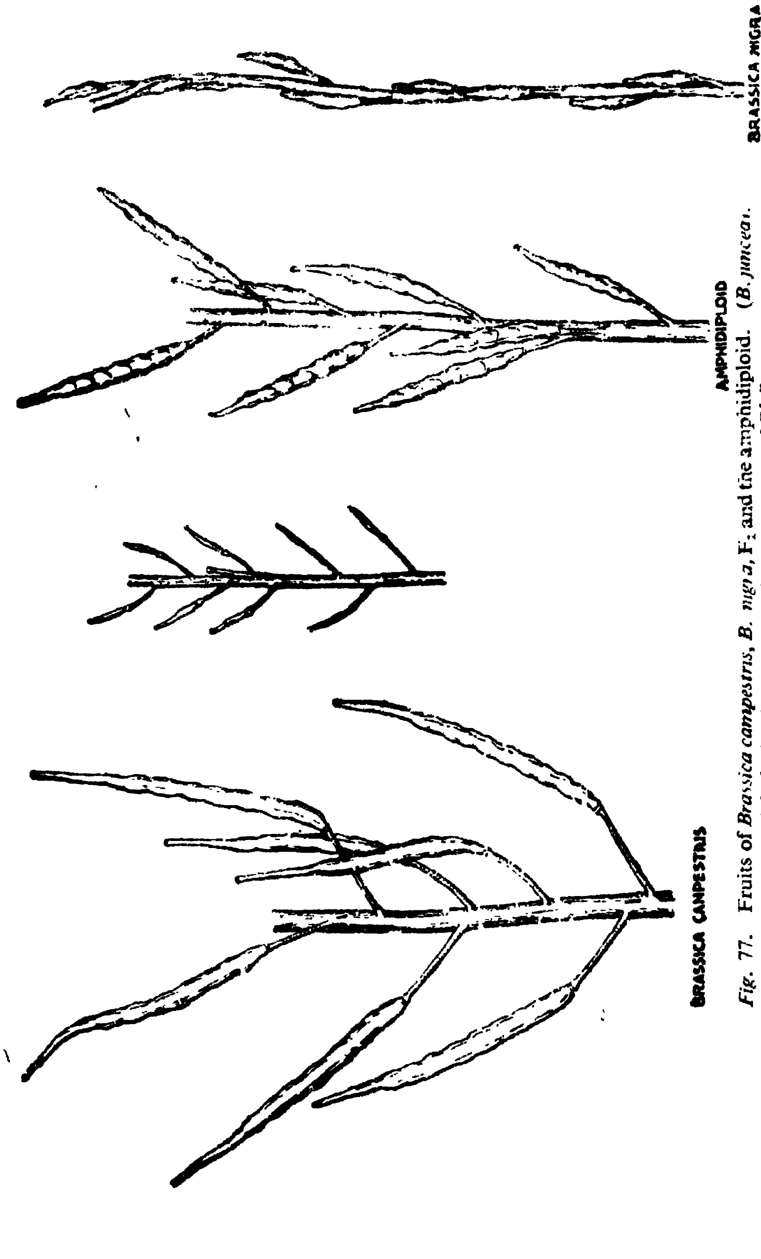


Fig. 77. Fruits of *Brassica campestris*, *B. nigra*, F_1 and the amphidiploid. (*B. juncea*).
(*With the kind permission of Ind. Jl. Gen. and Pl. Br.*)

distributed at random in the first division. This resulted in cells with varying chromosome numbers. In the F_1, few seeds were produced by chance and an examination of the plant from these seeds showed that they contained 36 chromosomes instead of 18 as in the hybrid. These fertile F_2 progenies were tetraploids. At meiosis pairing was regular and the plant was fertile. This plant showed foliage like radish and root like cabbage. The fruit was peculiar: it resembled the cabbage in its lower portion and the radish in its apical portion. The tetraploid breeds true and segregation of characters is absent.

The work done in the artificial synthesis of *Brassica juncea* which is now proved to be amphidiploid is discussed here as an example.

The F_1 of the cross *Brassica campestris* (n = 10) × *B. nigra* (n = 8) shows 18 chromosomes in somatic cells. The reciprocal cross completely failed. The hybrid is more or less intermediate between the parents in many of morphological characters, but it was highly variable due to the heterozygosity of parents and was sterile. (Fig. 77).

At meiosis, generally bivalents and univalents, and occasionally trivalents and quadrivalents were noticed due to allosyndesis, (Fig. 78).

Fig. 78. Meiosis in F_1 hybrid between *B. campestris* and *B. nigra*. Metaphase I : (*a*) : univalents of F_1, (*b*) 10 univalents, 4 bivalents, (*c*) 8 univalents ; 3 bivalents and 1 tetravalent, (*d*) 12 univalents, 1 bivalent and 1 tetravalent. (*e*) 9 univalents, 3 bivalents and 1 trivalent, (*f*) a chromatin bridge and a fragment, (*g*) 2 chromatin bridges and fragments, (*h*) No chromatin bridge.

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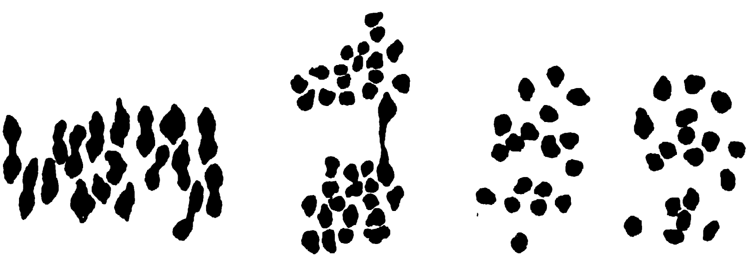
The frequency of occurrence of the different chromosome associations is shown in table 41.

At metaphase I the univalents were scattered while bivalents and trivalents lay on the equatorial plate. The bivalents were composed of unequal members showing allosyndesis in this case. At anaphase I, the disjunction of bivalents was not normal and hence chromatin bridges were frequently noticed. Formation of restitution nucleus was common. At metaphase II univalents and divided halves of univalents were noticed. Anaphase II was irregular.

TABLE 41.

Association.	Number.																		
	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Univalents ...	...	1	...	...	1	...	2	1	16	1	13	5	21	..	29	...	19	...	12
Bivalents ...	...	12	19	36	22	13	15	2	2	...	...	...	...	...	...	...	...	...	...
Trivalents ...	112	8	1	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
Quadrivalents ...	118	3	...	...	...	...	...	...	...	...	...	...	...	..	...	...	...	...	...

Due to these irregularities, empty and variable sized pollen grains were seen in indehiscent anthers. The hybrids were highly sterile and on open pollination set few seeds which proved to be crosses with *B. nigra* (n—8), *B. campestris* (n—10) or *B. juncea* (n—18) and the progenies showed 2n—26, 28 and 36 chromosomes respectively. It is therefore evident that unreduced gametes of the hybrid (2n—18) were fertilised by the reduced gametes of these three species.



1 2 3

Fig. 79. Amphidiploid *B. campestris* *B. nigra* (2n - 36) (1). Metaphase I (2) Anaphase I showing a bridge (3) Metaphase II.

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The amphidiploid of the cross was produced by colchicine treatment of one of the buds. Seeds from the amphidiploid bred true and the progenies were fertile and they very closely resembled the naturally existing species *B. juncea*. The following table shows the characteristics of the parents, F_1 and amphidiploid. (Fig. 79.)

TABLE 42.

Character.	B. campestris.	B. nigra.	F_1.	Amphidiploid (F_1, doubled).
Habit	Medium height dichotomously branched.	Fairly tall, branches much spreading.	Plants of varying height, spreading branches.	Fairly tall with spreading branches.
Stem : leaves	Amplexicaul, slightly lobed, pale green, glaucous without hairs.	Petiolate, much lobed, deep green, non-glaucous with stiff hairs.	Short petioled much lobed, green, slightly glaucous with hairs.	Short petioled much lobed, green, slightly glaucous with hairs.
Floral leaves	Amplexicaul, obtuse, triangular.	Petiolate, lanceolate.	Sessile to petiolate, lanceolate.	Short petiolate, lanceolate.
Inflorescence	Long, non-branching, pedicels almost at right angles to the axis of inflorescence.	Short, branching, pedicels erect and parallel with the axis of inflorescence.	Medium, non-branching, pedicels oblique to the axis of inflorescence.	Medium to long generally non-branching, pedicels oblique to axis of inflorescence.
Flowers	Sepals spreading, petals broadly obovate with short broad claws, anthers, extrorse.	Sepals slightly spreading, petals narrowly obovate with slender claws, anthers introrse.	Intermediate : anthers ill developed.	Same as F_1 but slightly bigger, anthers with a tendency to become extrorse.
Siliqua	Long, cylindrical torulose in the early stages becoming more or less smooth later on.	Short, subtetragonal torulose.	Ill developed.	Medium slightly compressed torulose.
Seeds	Globose, slightly rugose.	Ovoid, rugose.	...	Globose, rugose.

The fertility of the amphidiploid in the first two generations was low (30%—60%) but in the third generation it was highly fertile (90%—100%). The low fertility in earlier generations was due to meiotic irregularities such as allosyndetic pairing and non-disjunction in anaphase I with chromatin bridge formation. These irregularities were eliminated in the third generation and the progenies were fertile. This amphidiploid has very close resemblance to the naturally existing species *B. juncea* except for minor differences. Thus it is clear that *B. juncea* is amphidiploid. New species are thus found to arise by allopolyploidy. Other examples are (1) *Nicotiana* species (2) *Triticum* species (3) *Gossypium* (4) *Spartinia townsendii* (5) *Galeopsis tetrahit* (6) *Primula kewensis* (7) *Crepis artificialis* (8) *Raphanobrassica.*

9. Analysis of polyploids.—Polyploids occurring in Nature have arisen either within the species or from hybrids between species. Experimental production of polyploids has also resulted in the artificial creation of new species not hitherto existent in Nature, e.g., *Primula kewensis, Crepis artificialis.* By the modern experimental technique it is also possible in a few cases to artificially synthesise the naturally existing species, such as *Galeopsis tetrahit, Brassica juncea.* In many other cases, cytological investigations have led to an understanding of the probable mode of origin of the naturally existing species and such studies have given a clear understanding of the degree of relationship between the various species.

The cytological analysis of the degree of relationship between different species is based on the pairing behaviour of chromosomes during meiosis in the hybrids. The main principles governing chromosome pairing are (i) pairing is between similar chromosomes, (ii) chromosomes pair at regions where they are similar ; at regions where they are dissimilar they do not pair, (iii) at any one region, pairing is strictly confined to two chromatids.

When species A is crossed with species B, the hybrid contains one haploid complement from each one of the parents. During meiosis in such hybrids, the pairing depends upon the degree of relationship between the two parental species. If they are closely related, chromosomes of species ' A ' pair with chromosomes of species ' B ' and this is termed *allosyndesis.* The number of bivalents so formed will depend upon the number of chromosomes that bear similarity. Allosyndesis therefore indicates that A and B had a common origin in a progenitor which may be extant or extinct. If A and B have differentiated divergingly and widely, step by step in course of time they lose the similarity or homology of their chromosomes. They differentiate between themselves and also from their progenitor. When differentiation is complete,

allosyndetic pairing becomes impossible and the hybrid shows univalents only during meiosis. When allosyndetic pairing is not possible in the hybrid, the chromosomes of A may pair between themselves and chromosomes of B also pair within themselves. This is termed *autosyndesis*. Autosyndesis therefore reveals that the haploid chromosome complement of the species is not truly haploid but that some or all the chromosomes contain distant homologous *within* the complement. This is possible when the species A or B is not truly diploid in origin but is a polyploid species. Autosyndesis is therefore an evidence for the polyploid nature of the parental species.

Another cytological observation which is helpful is '*secondary pairing*'. At the first metaphase of meiosis in some cases, bivalent chromosomes of similar size and shape lie close to each other but there is no contact with each other. The forces of attraction and repulsion come to a balance when these similar chromosomes are at some distance from one another. This secondary pairing may continue to be evident even in the second division of meiosis. It is variable in its occurrence. Secondary pairing becomes of importance where the relationships between the chromosomes of a species cannot be analysed by other methods.

The foregoing cytological phenomena are utilised in the analysis of the polyploid species. Analyses in respect of some plants are discussed below :

Nicotiana sp.—There are about 20 distinct species of which the majority have n—12 or 24. In the hybrids the following pairing behaviour is noticed.

Close pairing.—

N. paniculata (n—12)	×	*N. rustica* (n—24)
N. sylvestris (n—12)	×	*N. Tabacum* (n—24)
N. tomentosa (n—12)	×	*N. Tabacum* (n—24)
N. Rusbyi (n—12)	×	*N. Tabacum* (n—24)
N. tomentosa (n—12)	×	*N. Rusbyi* (n—12)

No pairing.—

N. sylvestris (n—12)	×	*N. tomentosa* (n—12)
N. glutinosa (n—12)	×	*N. bigelovii* (n—24)
N. sylvestris (n—12)	×	*N. Rusbyi* (n—12)

Goodspeed and Clausen have studied the relationships between the chromosome complements of the different species. Their conclusion in respect of a few species is represented in Fig. 80.

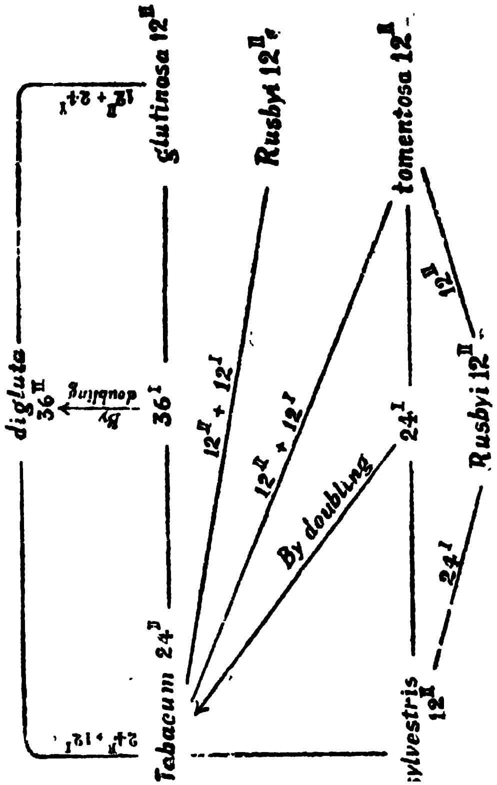

Fig. 80. Chromosome pairing in interspecific crosses in *Nicotiana*.

Taking the case of *N. Tabacum*, it is found that there is no pairing among the 24 chromosomes of the haploid. When this species is crossed with *N. sylvestris* there are 12 bivalents and 12 univalents revealing that 12 chromosomes of *N. sylvestris* are homologous with 12 out of 24 chromosomes of the *N. Tabacum*. Similarly when *N. Tabacum* is crossed with *N. tomentosa* there are 12 bivalents and 12 univalents showing that 12 chromosomes of *N. tomentosa* pair with 12 out of 24 chromosomes of *N. Tabacum*. When *N. sylvestris* is crossed with *N. tomentosa* there are 24 univalents revealing non-homology between the two chromosome complements. Therefore it is clear that *N. Tabacum* consists of 12 chromosomes closely homologous with the 12 of *N. sylvestris* and another 12 homologous with the 12 of *N. tomentosa*. In other words, *N. Tabacum* has probably arisen by doubling of the chromosomes in the species hybrid *N. sylvestris* × *N. tomentosa*.

N. digluta is a synthetic species which arose by the doubling of chromosomes of the cross *N. Tabacum* × *N. glutinosa*.

The fertility of both *N. Tabacum* and *N. digluta* is due to autosyndetic pairing in the chromosomes of the doubled hybrid.

Wheat.—The known species of wheat fall into three groups in respect of their chromosome number.

TABLE 43.

Einkorn group $n = 7$.	Emmer group $n = 14$.	Vulgare group $n = 21$.
T. aegilopoides ...	*T. dicoccoides* ...	*T. spelta.*
T. monococcum ...	*T. dicoccum.* *T. durum.* *T. turgidum.* *T. polonicum.* *T. persicum.* *T. Timopheevii.*	*T. vulgare.* *T. compactum.* *T. sphaerococcum.*
Genom (A).	Genom (AB).	Genom (ABD).

(i) *T. polonicum* × *T. spelta*

T. turgidum × *T. compactum.*

T. durum × *T. vulgare.*

T. polonicum × *T. compactum.*

T. turgidum × *T. vulgare.*

The above crosses have been studied. At heterotypic metaphase, 14 bivalents and 7 univalents are generally noticed. Bivalents separate normally but univalents lag behind.

(ii) *T. dicoccum* × *T. monococcum.*

T. aegilopoides × *T. dicoccum.*

In the above two crosses, 4 to 7 lose bivalents, and univalents are seen. In *T. spelta* × *T. aegilopoides* 10 bivalents and 8 univalents are noticed.

(iii) *Aegilops cylindrica* × *T. vulgare.*

A. cylindrica × *T. spelta.*

The hybrids of these two crosses show 7 bivalents and 21 univalents.

(iv) *Aegilops ovata* × *T. monococcum.*

A. cylindrica × *T. dicoccum.*

In the hybrids of these crosses no bivalents are noticed.

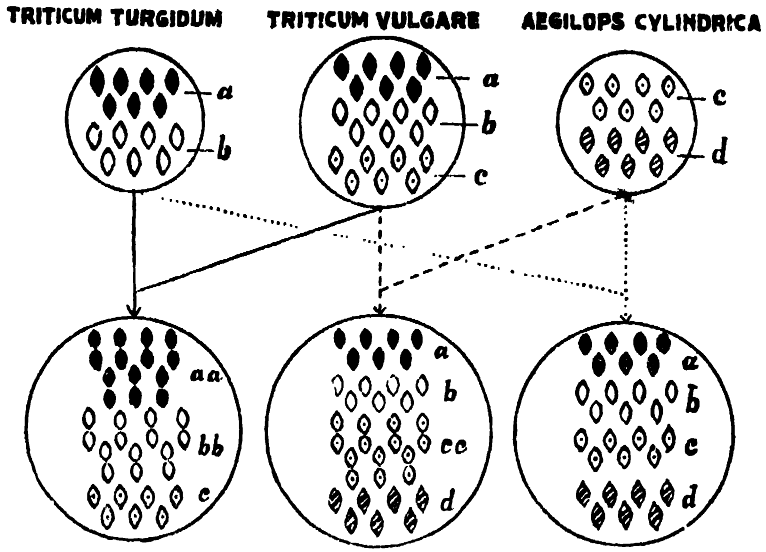

Fig. 81. To illustrate the formation of bivalents and univalents in interspecific and intergeneric crosses in wheat.

(v) Hybrids between the species falling within any group are fully fertile and show only bivalents at meiosis. The hybrids between the Einkorn and Emmer groups are triploids. They generally show 7 bivalents and 7 univalents. The hybrids between Emmer and vulgare groups are pentaploids and at meiosis show 14 bivalents and 7 univalents. (Fig. 81).

It is interpreted that the three groups contain three sets of chromosome complements A, B, D, each consisting of 7 chromosomes as explained below :

Emmer group is an allotetraploid from hybrids between an Einkorn species (A genom) and another species (with B genom). Cross between Emmer (AB genom) and a species of Aegilops (genom D) by hexaploidy has given rise to *vulgare* group.

The foregoing scheme of evolution of *Triticum sp.* is reduced to greatest simplicity in presentation. The various chromosome sets have differentiated gradually and the similarity between the genoms may vary by degrees. In short, the evolution of the various species has been by allopolyploidy and the differentiation of the genoms themselves by mutation of genes and structural changes in the chromosomes.

Brassica juncea.—The amphidiploid nature of this species has been already discussed. When *B. juncea* is crossed with *B. campestris*, the hybrid shows $10_{II} + 8_{I}$ at meiosis. The bivalents are formed by the association of 10 *campestris* chromosomes with 10 *juncea* chromosomes, the remaining 8 chromosomes of *juncea* form the univalents.

When *B. juncea* is crossed with *B. nigra* the hybrid forms $8_{II} + 10_{I}$. The 8 chromosomes of *B. nigra* form bivalents with 8 chromosomes of *B. juncea* and the balance of 10 chromosomes of the latter form 10 univalents. This

shows that in *B. juncea* there are two genoms (*a*) 8 chromosomes homologous with those of *B. nigra* (*b*) 10 chromosomes homologous with those of *B. campestris.* Autosyndesis is completely absent within the two chromosome complements and therefore univalents are left behind in the hybrids. This method of pairing is termed " *Drosera scheme* " of pairing and is useful in the analysis of hybrid species.

Gossypium sp.—The known species under *Gossypium* fall under two groups (1) the old world group showing n—13-(2) the New World group with n—13 or 26. In both the groups there are cultivated and wild forms.

The meiotic behaviour in the hybrids between the various species is summarised below :

(i) *G. herbaceum* × *G. arboreum var. neglectum*
13 bivalents are formed.

(ii) *G. harknessii* × *G. armourianum*
13 bivalents are formed.

(iii) *G. hirsutum* × *G. armourianum*
13 bivalents and 13 univalents formed.

(iv) *G. barbadense* × *G. harknessii*
13 bivalents and 13 univalents are formed.

(v) *G. barbadense* × *G. sturtii*.. 0—4 bivalents
× 31—39 univalents are formed.

(vi) *G. sturtii* × *G. armourianum*

(vii) *G. sturtii* × *G. harknessii*

(viii) *G. davidsonii* × *G. sturtii*

} 0—6 bivalents and 14—26 univalents are formed.

(ix) *G. arboreum Var. neglectum* × *G. stocksii.* Average of 7 bivalents and 12 univalents are formed.

The cultivated New World species (n—26) contain (*a*) 13 chromosomes which are homologous with the 13 chromosomes of the New World wild species and (*b*) another 13 chromosomes which are homologous with the 13 chromosomes of the Old World cultivated forms. The present New World cottons, such as Upland, Sea Island, Egyptian and Bourbon, are therefore allotetraploids with one Asiatic component, ancestral to *arboreum* or *herbaceum* and one New World component ancestral to *aridum, raimondii, Thurberi, armourianum,* or *harknessii.* Harland (1940) crossed *G. arboreum* with *G. thurberi* and by doubling the chromosomes in F_1, synthesised an amphidiploid closely resembling the New World tetraploids. This synthetic tetraploid freely hybridises with the naturally existing tetraploids.

On the basis of such analyses, Beasley designates the genoms of the various species as indicated below :

G. herbaceum	...	... $2A_1$
G. arboreum Var neglectum		... $2A_2$

G. Thurberi	$2D_1$
G. hirsutum	$2(AD)_1$
G. barbadense	$2(AD)_2$
G. sturtii	$2C_1$

... addition of com
...id complements on doubling of the hybrid ... plex chromos...
...ges may take place before doubling. It has be... that tris...
...etrasomic forms arise from sterile triploids. ... is al...
...ncy to overcome this barrier by doubling of chro... complem...
...s and pears belong to the family *Rosaceae* with basic number as 7.
...*omoideae* section the basic number is 17 and this latter number seem...
...been derived from a trebly trisomic diploid which becomes balanced...
...loidy. This is known as *secondary polyploidy*. This is indicated...
...ex segregation of factors and by secondary pairing of chromoso...
...rly from the formation of bivalents in haploid, quadrivalents in dipl...
...exivalents in triploids of *Oryza sativa*, it is concluded that the cultiva...
...f *O. sativa* has arisen by secondary polyploidy of an unknown spe...
—5. (2n + 2) of this unknown species has formed the basic num...

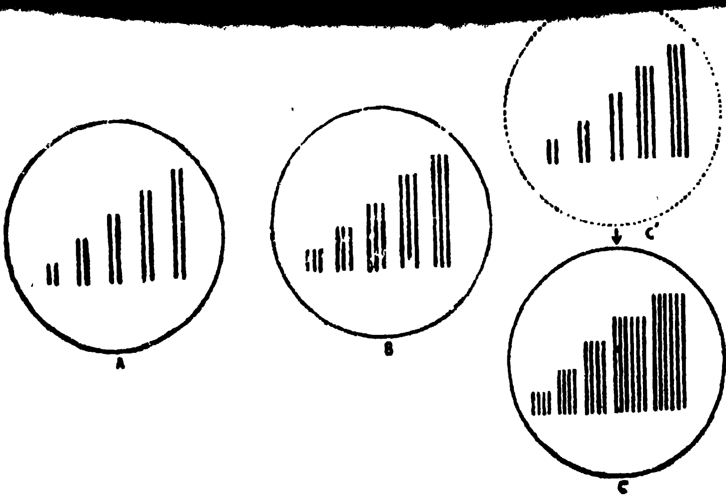

Fig. 82. Diagrammatic illustration of the probable origin of rice (*Oryza sativa*). A is the diploid ancestor, with *n* 5 (now extinct). B is a triploid from A and it had formed the basis for the polyploid species under the section *Zizanineae*. C shows an aneuploid with 12 chromosomes arising from 'A'. This has formed the basis for the polyploid species under the section *Oryzineae*.

In this case odd chromosomes have been added to the normal complement to constitute the basic number of the new polyploids.

Secondary polyploids may also arise by loss of chromosomes. *Crepis artificialis* is an instance. The F_1 of *C. biennis* (n—20) × *C. setosa* (n—4) shows 10 pairs of *biennis* complement by autosyndesis and the 4 *setosa* chromosomes are univalents. By selfing, a progeny with 10 pairs of *biennis* a... pairs ... a, was obtained. The latter pairs arose by loss of 2 se...

The role of sec... polyploidy may well be explained by taking O... xample.

Hutchi... ssified *Oryzeae* into two sections (1) *Oryzineae* (2) *Ziza*... cytogenetics of the following species were studied to find out their ... tionship :

Oryzineae. Basic number = 12

1.	*Oryza sativa*	24
2.	*O. glaberrima*	24
3.	*O. officinalis*	24
7.	*O. minuta*	48
8.	*Leersia hexandra* .	48
9.	*L. oryzoides*	...

Zizanineae. Basic number = 5

10.	*Zizania aquatica* ..	30
11.	*Z. latifolia*	30
12.	*Zizaniopsis miliaceae* ..	

Secondary association of chromosomes in *O. sativa* is noticed. A maximum association of 2 groups of 3 bivalents and 3 groups of 2 bivalents were noticed by Nandi (1936). Autosyndesis in the species confirms the hypothesis that the species is of polyploid origin.

The species of *Zizanineae* are hexaploids with 5 as basic number. Oryzineae has basic number 12 which is derived from 5 by secondary polyploidy. While *Zizanineae* has retained the basic number 5 and formed polyploid species, *Oryzineae* has developed a secondary basic number and formed polyploid species. The species in the latter group have been formed by structural changes in the chromosomes as evidenced by non-pairing in the meiosis of the hybrid *O. officinalis* × *O. sativa*.

10. Pentaploids.—The somatic cells in pentaploids show 5n chromosomes. Pentaploids have been artificially produced.

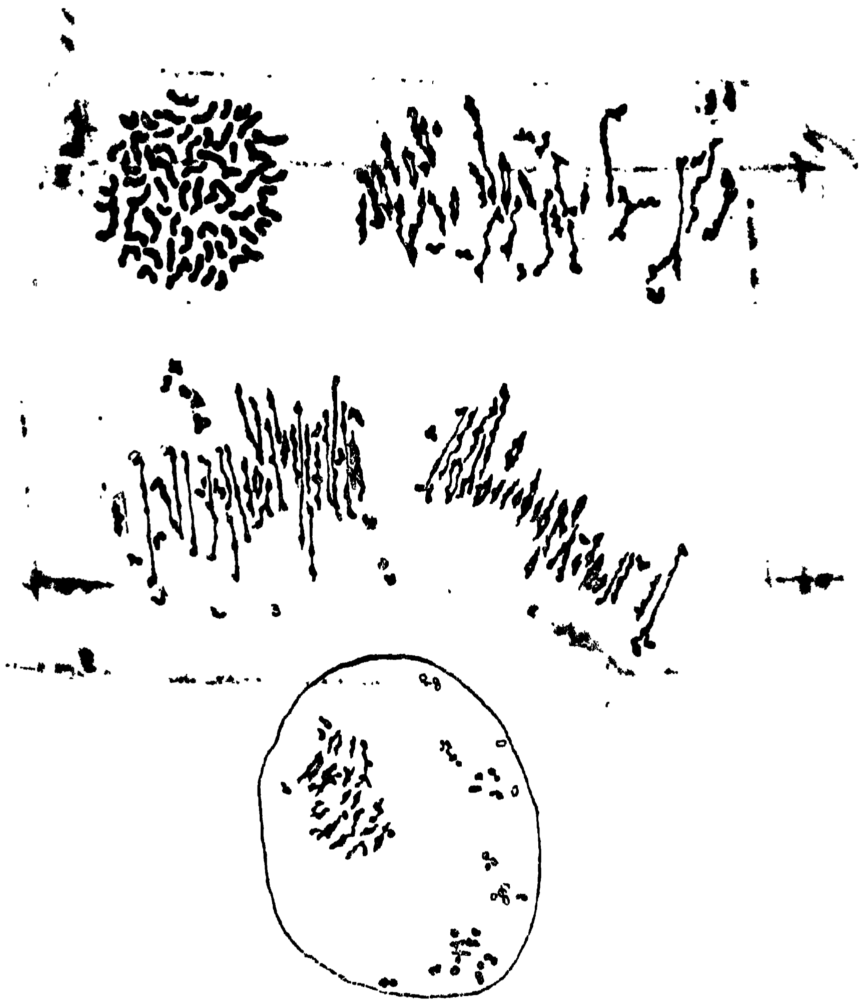

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Fig. 83. Pentaploid cotton B.C. 307. (1) Somatic metaphase (2) Meiosis. Metaphase (I) showing 17 univalents, 15 bivalents and 6 trivalents. (3) Metaphase (I) showing 15 univalents, 19 bivalents and 4 trivalents (4) Metaphase I showing 6 univalents, 25 bivalents, and 3 trivalents. (5) A binucleate P.M.C. showing, one nucleus undergoing normal division and the chromosomes of the other are scattered.

In the course of hybridisation work in cotton (1943) the American and the Asiatic types were crossed and back-crossed at Surat.

The following are some of the crosses which yielded pentaploid (2n—65) progenies.

B.C. 201 :	*G. barbadense*	× *G. herbaceum*	F_1	× *G. barbadense*
B.C. 236 :	*G. hirsutum*	× *G. herbaceum*	F_1	× *G. hirsutum*
B.C. 307 :	*G. hirsutum*	× *G. arboreum*	F_1	× *G. hirsutum*
B.C. 259 :	*G. herbaceum Var. frutescens*			× *G. barbadense*
			F_1	× *G. hirsutum*

In metaphase I of meiosis, univalents, bivalents and trivalents are seen. (Fig. 83.) In some cases chromosome associations of higher valencies are also present ; in some cells pairing is completely absent. Though there are 3 sets of one genom with the maximum possibility of 13 trivalents, the latter varied from 1 to 10.

At anaphase II the common distribution is 30—35. Hybridisation between the American (n—26) and the Asiatic (n—13) cottons yield triploid (2n—39) progenies. Unreduced gametes of these triploids when fertilised by the American back-cross parent (n—26) result in pentaploid progenies (2n—65). Pentaploids may also arise by fertilisation of n—13 egg of a triploid by unreduced pollen (n—52) of the American parent. The pentaploids resemble the auto-triploids in the most frequent trivalent chromosome association.

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Fig. 84. Meiosis in Hexaploid cotton. (1) Metaphase I in hexaploid showing 3 univalents, 30 bivalents, 1 trivalent and 3 tetravalents. (2) Metaphase II in hexaploid. (3) Anaphase I showing 3 bridges.

11. Hexaploids.—Triploids (3n) when doubled yield hexaploids (6n). In cotton, by doubling the hybrids between the 13 and 26 chromosome groups, hexaploids were artificially produced (1944). The parentage of some of the hexaploids is shown in table 44 (Fig. 84).

TABLE 44.

Hexaploid.	Parentage. N—13.	Parentage. N—26.
S. 28—1	*G. herbaceum* : 1027 *ALF* * 2A_1	*G. hirsutum* : Co_2 : 2 $(AD)_1$.
S. 31—1	Do.	*G. barbadense* (Sea Island) : 2 $(AD)_2$.
S. 34—1	Do.	Do.
S. 39—1	*G. arboreum* : 2A_2	*G. hirsutum* : 2 $(AD)_1$.
Wild American × cultivated American ...	*G. thurberi* : 2D_1	*G. barbadense* : Boss III-16 2 $(AD)_2$.
Do. ...	*G. armourianum* : 2D_2	*G. barbadense* : 2 $(AD)_2$.
Wild African × cultivated American ...	*G. anomalum* : 2B_1	*G. hirsutum* : Co_2 : 2 $(AD)_1$.
Do. ...	Do.	*G. barbadense* Sind Sea Island 2—4 : 2 $(AD)_2$.

* Symbols for genoms that constitute the species complement (*vide*) Section 8.

The mean values for chromosome association in the hexaploid cottons derived from cultivated American types × Asiatic types are shown in table 45.

TABLE 45.

Hexaploids.	Univalents.	Bivalents.	Trivalents.	Quadri-valents.	Penta-valents.	Hexa-valents.
S. 28—1 ...	1·29	29·50	0·88	3·58	...	0·13
S. 31—1 ...	3·13	34·13	1·38	0·63	...	...
S. 34—1 ...	1·13	35·13	1·38	0·63	...	...
39—1 ...	1·50	28·50	1·13	2·38	0·13	1·00

Bivalent association is the most frequent one.

The progenies of hexaploids show varying chromosome numbers. This is to be expected due to the fact that multivalent chromosome association during meiosis results in the formation of gametes with plus or minus deviation from the expected 3n number (Fig. 84). In table 46, is shown the chromosome distribution in the progenies of hexaploids.

TABLE 46.

Hexaploid parent.	Somatic chromosome number in the progenies of hexaploids.									Total No of plants studied.
		75	76	77	78	79	80	81	82	
1. S. 28—1	...	...	...	2	12	2	1	...	...	17
2. Co_2 × *G. armourianum* ...	...	...	1	1	8	...	...	2	...	12
3. *G. barbadense* × *G. armourianum*	1	...	...	...	6	...	...	...	1	8
4. *G. barbadense* × *G. anomalum.*	...	...	...	...	2	...	...	...	...	2
5. *G. hirsutum* × *G. anomalum* ...	...	...	...	...	10	...	3	1	...	14

The greater frequency of progenies with 78 somatic chromosomes indicates that the progenies are mostly hexaploids.

12. Haploids.—Haploidy in flowering plants was first reported by Blakeslee *et al* (1922) in *Datura stramonium.* Since then haploids in various other plants have been recorded. They were either spontaneous in origin or were induced under artificial conditions. The following list shows some of the plants in which haploids have been recorded and studied.

TABLE 47.

1. *Brassica campestris*	 10	(Figs. 88, 89)
2. *B. napella*	 19	
3. *Campanula persicifolia*	 16	
4. *Datura stramonium*	 12	
5. *Gossypium barbadense*	 26	
6. *G. Davidsonii*	... ...	
7. *G. hirsutum*	 26	
8. *Hordeum vulgare*	... ...	
9. *Lycopersicum esculentum*	 12	
10. *Nicotiana glutinosa*	 12	
11. *N. Langsdorffii*	... ...	
12. *N. sylvestris*	... ...	
13. *N. tabacum*	... ...	
14. *Oenothera franciscana*	 7	
15. *O. Hookeri*	 7	
16. *O. Lamarckiana-gigas*	 14	
17. *O. rubricalyx*	 7	
18. *Oryza sativa*	 12	
19. *Portulaca grandiflora*	 9	
20. *Triticum compactum*	 21	
21. *T. dicoccum*	 14	
22. *T. monococcum*	 7	
23. *T. persicum*	... ...	
24. *Zea mays*	 10	

Haploids may arise by any one of the following processes :—

(1) The reduced egg develops without fertilisation as noted in *Solanum*. This is termed as *female parthenogenesis*. The stimulus for such a development may be provided by foreign pollen.

(2) Male nucleus may enter the egg and the egg may be stimulated to develop without the participation of egg nucleus. This is termed *male parthenogenesis* or *androgenesis*.

(3) Of the four reduced cells of the tetrad from EMC more than one may develop. Of these two, one may be fertilised and the othe may develop parthenogenetically, *e.g.*, in rice one such instance was reported. One haploid and the other diploid seedling arose from a seed. The haploid one arose by parthenogenetic development of one more egg cell from the tetrad formed by EMC. Polyembryony in rice is shown in Fig. 85.

(4) One of the reduced cells in embryo-sac such as synergid or antipodal may develop parthenogenetically.

(5) The stimulation for parthenogenetic development may arise by both the generative nuclei fusing with the polar nuclei giving rise to tetraploid endosperm cells (instead of normal triploid) and the egg develops without fertilisation. This has been noticed in *Triticum compactum*.

(6) When X-rayed pollen was dusted on to the stigma parthenogenetic development was noticed occasionally in *Triticum monococcum* and *Nicotiana rustica*.

(Photo from Paddy Specialist).

Fig. 85. Polyembryony in rice. Note the four seedlings from a single seed.

(7) Pollen from widely related species may provide the necessary stimulation. Pollen of *Datura ferox* when dusted on to the stigma of *D. stramonium* induces parthenogenesis in the latter.

(8) Application of low temperature to the flower may stimulate parthenogenetic development of the ovary.

All the above methods of origin of haploids can never be said with certainty to be specific in effect. So far no particular method has been found for inducing haploidy.

In their appearance, the haploids are reduced morphological replicas of the diploid. They are less vigorous and highly sterile. Their pollen grains are variable in size and are empty of contents. A small proportion of functional pollen grains may be formed by non-reduction in P.M.C. Diploids that arise by doubling of haploid complement of chromosomes provide interesting genetical material in that they are perfectly homologous. The haploid is maternal in appearance in maternal parthenogenesis and paternal in androgenesis. In some cases the haploid may not show any reduction in size or form or they may differ from the diploids in respect of few characters only such as sterility, leaf or flower in size and vigour.

Meiosis in haploids is irregular. In the dividing E M.C. and P.M.C. univalents appear. Absence of homology between the chromosomes of the haploid set, leads to non-pairing between the chromosomes. Regular equatorial plate is not formed at first division and the chromosomes lie scattered on the spindle. At anaphase I more than two groups with varying number of chromosomes are formed. Homotypic division is fairly regular and macro and microspores with incomplete genoms are formed. Divi ions in E.M.C. and P.M.C. are generally similar or may differ in small details.

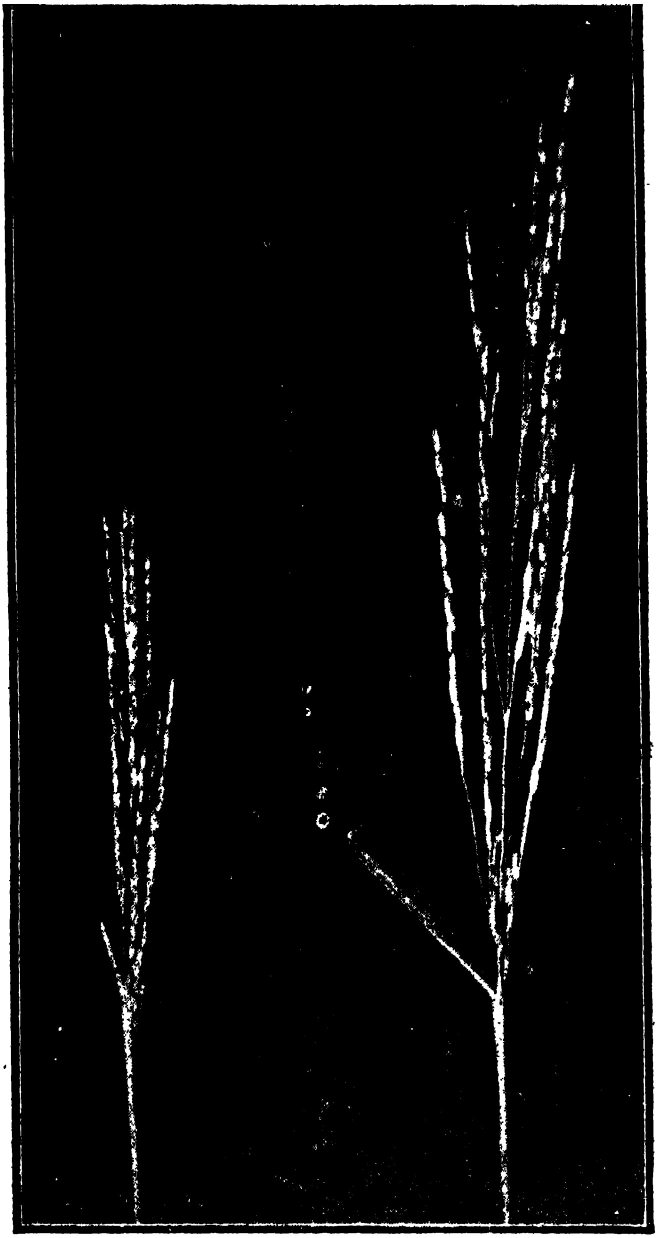
Cytology of haploid rice.—As an example for meiotic irregularities in haploids, cytological observations made on a haploid rice (1934) (Figs. 86, 87 and 90) are summarised here. In a pure line, the haploid occurred as a twin seedling from the diploid.

(*Photo from Paddy Specialist*).

Fig. 86. Haploid and diploid rice.

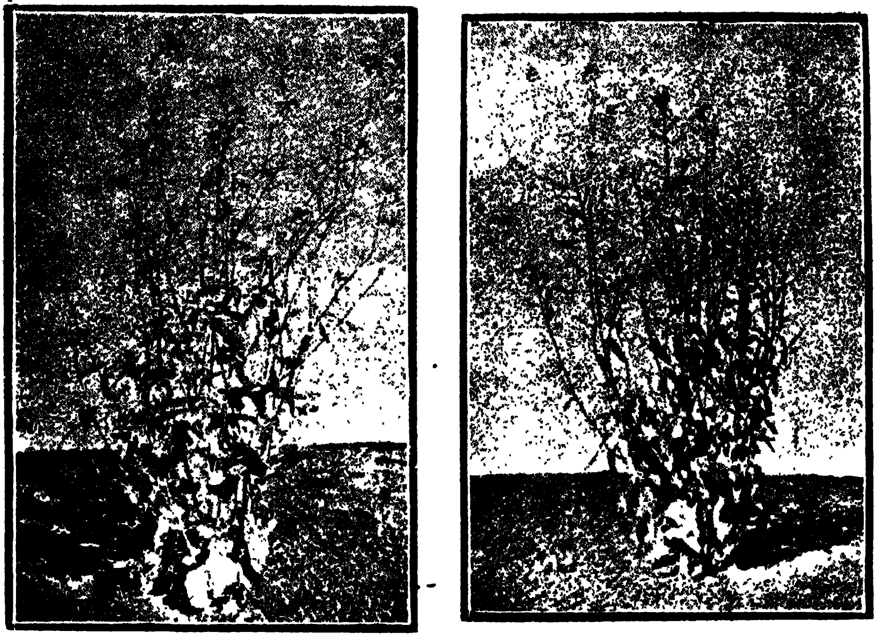
Pollen mother cells were fewer and smaller. At diakinesis homologous pairing was absent and 12 univalents were scattered. A single nucleolus was present. Later stages of cell division were irregular. At anaphase I, the chromosomes separated to the two poles at random. The distributions were

11-1, 10-2, 9-3, 8-4, 7-5, 6-6. Sometimes the spindle was crescent shaped and the chromosomes lay scattered on the spindle. Finally, 2-3 nuclei may be formed.



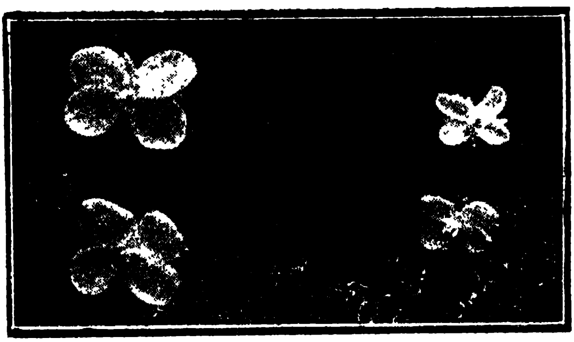
(*Photo from Paddy Specialist*).

Fig. 87. Earheads from haploid and diploid rice.



(*With the kind permission of Curr. Sc.*)

Fig. 88. *Brassica campestris*: Diploid and haploid.



(*With the kind permission of Curr. Sc.*).

Brassica campestris: Flowers from diploid and haploid.

Monads resulting from the suppression of both the divisions were not seen. Viable pollen grains were not formed (Fig. 90).

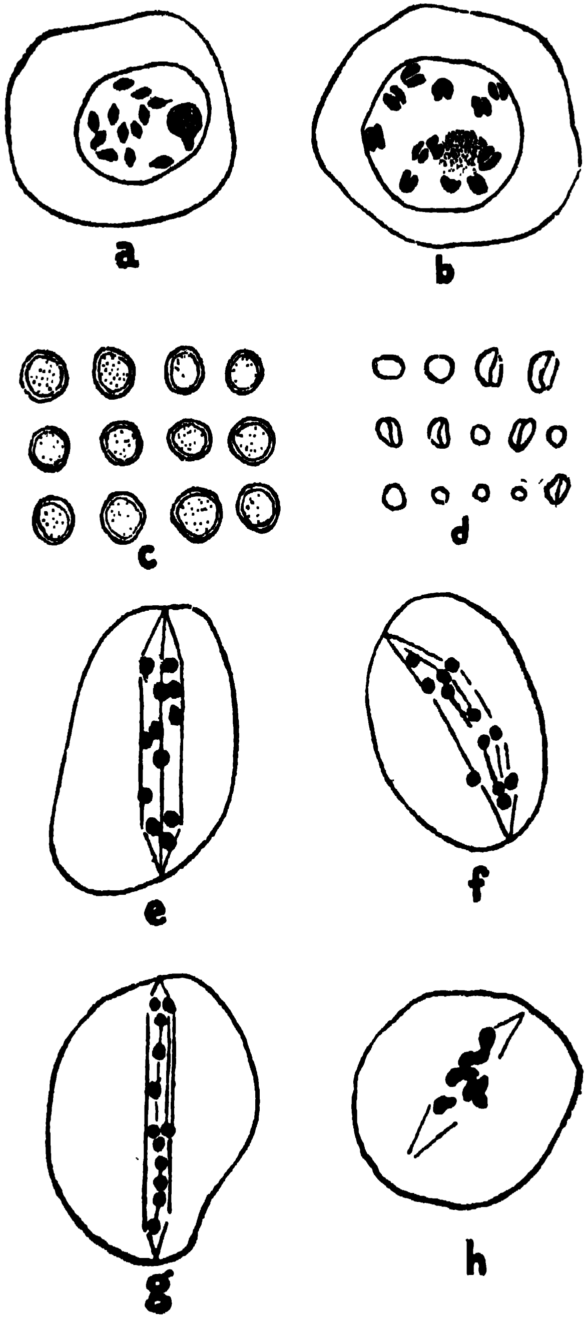


Fig. 90. Meiosis in a haploid rice plant. (a) Prophase corresponding to diakinesis with 12 univalents. (b) Diakinesis in a diploid with 12 bivalents. (c) Pollen grains of diploid. (d) Pollen grains of haploid. (e, f, g). Heterotypic anaphase showing laggards and disposition of spindles. (h) failure of first division and the collection of chromosomes in a single nucleus.

(*After Ramiah et al*).

Under the following exceptional circumstances haploids may give rise to progenies.

(1) Dyads with n chromosomes may be formed due to 0-n distribution.
(2) The heterotypic division may be completely omitted.
( ) Univalents may divide in both the divisions of meiosis.
(4) Monads with n or 2n chromosomes may be formed.

The haploids are generally sterile or on open pollination, under circumstances stated above generally give rise to diploid progenies. In *Nicotiana tabacum* some pollen grains having one or two chromosomes less than the haploid number were functional and on fertilising a normal egg gave rise to *monosomics* (2n-1). A complete set of monosomics may be established in such cases where, in each case a different chromosome from the haploid set may be absent. A comparison of the monosomic form (2n-1) with the corresponding trisomic form (2n+1) will prove interesting for Mendelian analysis of the characters.

Therefore it is evident that the pseudo-reduction in haploids leads to formation of gametes with variable number of chromosomes. Gametes with the complete haploid complement only function but in some cases gametes with one or two chromosomes less may also function. The former gives rise to diploids and the latter to monosomics.

Haploids may be classified into (1) *mono-haploids* and (2) *Poly-haploids*. When haploids arise from truly diploid species, which are also termed as *basal species*, all the chromosomes are non-homologous to one another. When haploids arise from polyploids they are termed poly-haploids. The latter again fall into two categories. (1) allohaploids from allo-polyploids and (2) pseudo-haploids from autopolyploids. In allo-haploids two haploid sets one from each of the parental species are present. Pseudo-haploids are not true haploids because they really contain more than one haploid complement of chromosomes, *e g.*, a haploid from auto-tetraploid species contains 2n chromosome complements and therefore they are really diploids.

13. Polyploidy in Evolution.—A general review of chromosome numbers in the related species shows that they are in multiples of a number which is termed the basic number for the group, *e.g.*, 12 for *Solanaceae*. Polyploidy is found to be of wide occurrence in Nature. Polyploids generally arise directly by doubling of chromosome number. It may happen after species hybridisation or by doubling after the addition of a few chromosomes to the basic number. Cytogenetic investigations in *Nicotiana tabacum*, *N. rustica*, *Spartinia townsendii*, *Galeopsis tetrahit*, *Oryza sativa* and New World cottons have shown that these are polyploids of one type or another. In isolated instances such as *Brassica juncea*, *Galeopsis tetrahit*, *etc.*, the naturally existing species were artificially synthesised. If two species could be crossed and if the hybrid is fertile, then the chromosomes of the two species are of common origin and they still retain their homology. Autosyndesis in species crosses shows that the sets of chromosome complements are widely differentiated while allosyndesis show that they still retain their homology. Therefore by the extent of auto or allosyndesis taking place, the degree of relationship between the species may be established. The amount of differentiation will be inversely propor-

tional to the amount of allosyndesis. Thus, in the artificially synthesised *Brassica juncea* when it is crossed with *B. campestris*, $10_{11}+8_{1}$ are seen, while when crossed with *B. nigra*, $8_{11}+10_{1}$ are seen. This is termed *Drosera scheme of pairing* and this will be evident in cases where autosyndesis is absent.

Autopolyploidy increases sterility due to multivalent chromosome association especially in long chromosomes, whereas autopolyploidy with short chromosomes form bivalents due to pairing conditions. Immediately after the origin, of autopolyploidy they are generally sterile but in later generations fertility increases due to elimination of chromosomal irregularities. The increase in fertility in the auto-tetraploid *Cicer arietinum* is shown in table 48.

TABLE 48.

Season.	Percentage fertility.				
	36—45.	46—55.	56—65.	66—75.	76—85.
1939-40 ...	3	7	6	3	2
1940-41 ...	25	17	10	4	6

Even in amphidiploids a small percentage of sterility may be met with in initial stages but this is overcome in later generations as is shown in table 49 for amphidiploid *B. Campestris B. nigra.*

TABLE 49.

Generation.	Percentage of fertile pollen.						
	40.	40—49.	50—59.	60—69.	70—79.	80—89.	90—10.
1 ...	...	...	2	...	...	...	...
2 ...	4	11	2	...	...	...	...
3 ...	1	...	3	1	2	6	41

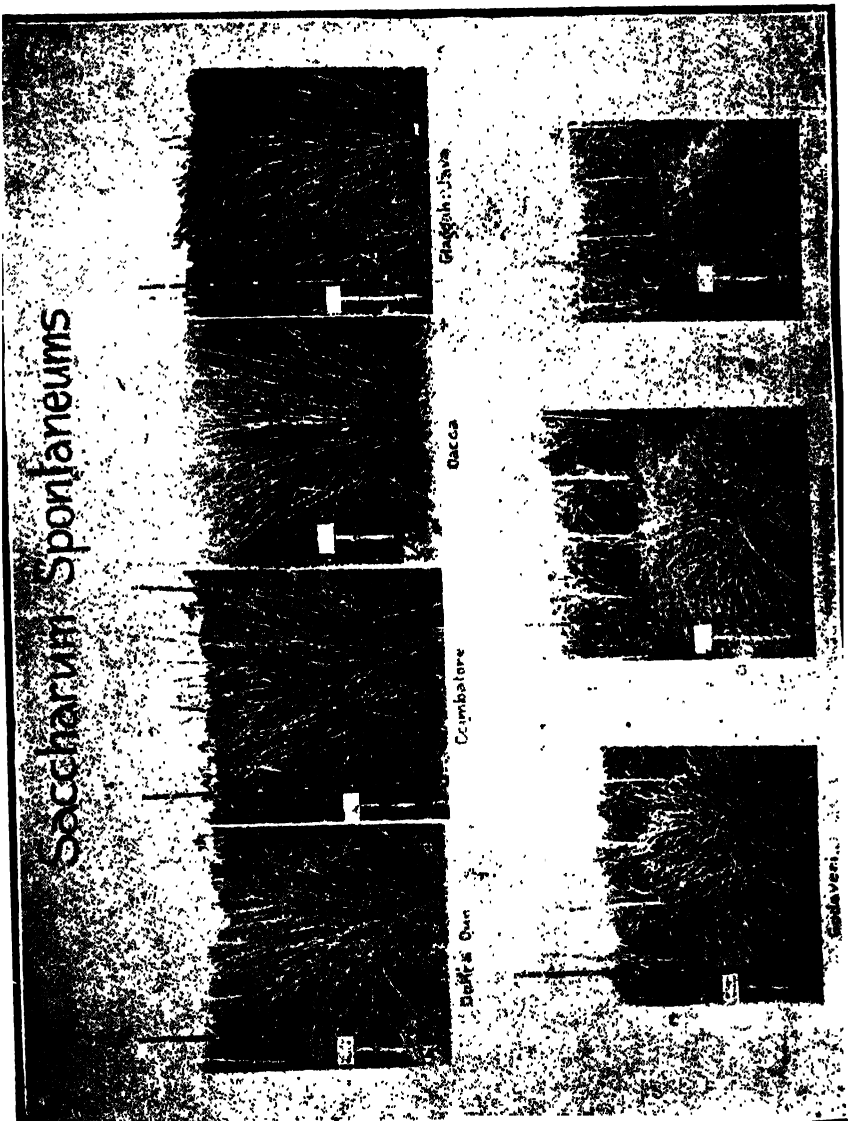
(Figures show frequency in the population studied.)

Newly evolved amphidiploids are not very stable under natural conditions and they are subjected to certain changes before they form stable species in Nature. In *N. tabacum* Clausen (1941) showed that elimination of duplications is one of the important steps.

The extra chromosomal complements in polyploids confer certain advantages to the species which are lacking in diploid forms. It has already been pointed out that in an autotetraploid, for example, the two extra sets of genes are available for mutation without seriously affecting the existing characteristics. If the mutation is deleterious it is immediately reflected in the progenies of diploids whereas in the case of polyploids the deleterious genes are buffered or sheltered by the presence of other normal allelomorphic genes. If the mutation is in favourable direction it adds to the selection value. Therefore,

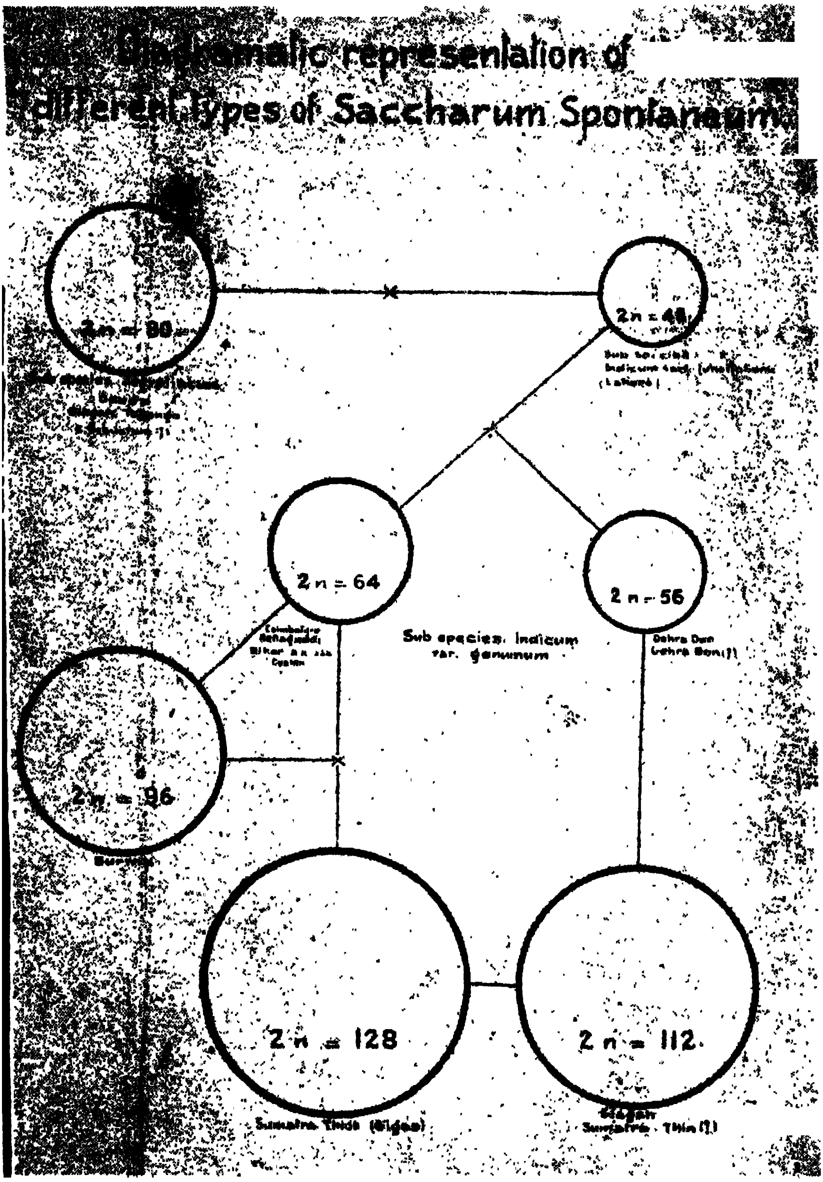
the polyploid forms are important from the point of view of evolution. In course of time autotetraploid behaves like a dip'oid by a series of mutational changes in the extra genes. As the mutivalent chromosome association is a great drawback, by differential changes between the extra chromosomal pairs, the polyploid not only gains new values but also in course of time behaves functionally as a diploid.

An increase in the chromosome number is followed by gigas nature of morphological characters. It is also followed by physiological systems which decide the geographical distribution of the species (Fig. 91, 92). This may be illustrated by the distribution of *Saccharum spontaneum.*



(With the kind permission of India Government. Photo from Sugarcane Expert).

Fig 91. *Saccharum spontaneum* from different localities.



(*With the kind permission of India Government. Photo from Sugarcane Expert.*)

Fig 92. Diagrammatic representation of the different types of *Saccharum spontaneum*.

S. spontaneum from	n
Himalayas	28
Bihar and Punjab	32, 36
Assam	40
Burma	48
Sumatra & Java	56, 60
gigas form from Sumatra	64

There is gradual increase in chromosome number from North-west to South-east in its distribution.

Muntzing (1936) showed that the annual forms give rise to perennial types by polyploidy. Even in artificially induced polyploids, flowering is delayed.

The small chromosomal changes that arise in polyploids slowly accumulate in course of time and finally it is genetically isolated from its diploid progenitor. Therefore the polyploid proves cross sterile with its progenitor and differentiates into new species.

15. Polyploidy in Breeding.—Increase in chromosome number appears to be one of the primary changes in the derivation of new species in nature. It has been pointed out that some new species have been synthesised by geneticists—*Primula kewen is*, *Crepis artificialis*, *Brassica juncea* are some examples. A plant breeder must take guidance from what happens in Nature. Therefore, recently many attempts have been made to induce polyploidy by colchicine treatment.

Originally no advancement should be made in interspecific hybrids due to their sterility but the possibility of artificially doubling chromosomes by colchicine treatment has opened out a great possibility for advances in breeding

Amphidiploids form a bridge between the species which do not cross *e.g.* the Asiatic cottons do not easily cross with the cultivated American types. *G. anomalum* (n—13) is a New World wild cotton. It crosses with the cultivated Old World (n—13) cottons such as *G. arboreum*. The hydrid of the cross *G. anomalum* (n—13) × *G. arboreum* (n—13) is sterile. When the hybrid was artificially doubled by colchicine treatment, the amphidiploid crosses freely with *G. hirsutum* (n—26). It is now possible by repeated back-crossing and raising a large number of hybrid progenies to select types that may combine the desirable characteristics of both the types. Similarly, Amin (1941) synthesised amphidiploids from the crosses *G. anomalum* × *G. arboreum*, *G. anomalum* × *G. Davidsonii and G. anomalum* × *G. herbaceum*. These were crossable with American types though the hybrids were sterile. Harland could get fertile hybrids in the cross (*G. arboreum* × *G. thurberi*) F_1 doubled × New World cotton.

Hitherto, when breeders resorted to species crosses, the hybrids proved sterile in many cases and no further crossing or selection work could be undertaken. But the present day possibilities for the artificial production of polyploids have opened out further scopes in breeding. The polyploids are fertile and they could be utilised in further breeding programmes.

The cultivated species of tobacco, *Nicotiana tobacum*, is susceptible to downy mildew and blue mould. Most Australian species are highly resistant but they are genetically distant from them. After crossing, sterility in F_1 is overcome by chromosome doubling. *N. glauca* contains an alkaloid anabasine which is more active than nicotine. Allotetraploid shows high percentage of the same and they are more vigorous.

(*With the kind permission of India Government from Ind. Fmg.*)

Fig. 93. The flower size in the Tetraploid (top) is greater than in the Diploid (bottom).

Because of greater number of genes in polyploids, the chances of different types of mutation occurring without any deleterious effect on the plant in Nature affords greater scope for variability. Similarly, heterosis persists at a

higher rate in polyploids than in diploids *i.e.* polyploidy conserves hybrid vigour. The scope of variability is further increased due to its easy cross-ability with different species. Structural changes are more likely to occur in polyploids than in diploids.

Where the breeder is dealing with asexually propagated plants such as sugarcane and garden flower plants (Fig. 93) and where the vegetative parts and not fruits or seeds are the economic products, gigas forms and large variations can be induced by polyploidy. Polyploidy in parental species also enables wide crosses to be attempted. Greater success is met with here than in diploid forms. Thus crosses of sugarcane (*Saccharum officinarum*) with *S. spontaneum*. *Sorghum durra* were possible due to the high degree of polyploidy of sugarcane.

STRUCTURAL CHANGES IN CHROMOSOMES

GENIC ARRANGEMENT—TYPES OF STRUCTURAL CHANGES—DELETION—DUPLICATION—SIMPLE TRANSLOCATION—RECIPROCAL TRANSLOCATION—INVERSION—EVOLUTIONARY SIGNIFICANCE.

1. **Genic Arrangement.**—Changes in the architecture of the gene molecule are described as 'gene changes'. Such changes are believed to be chemical rather than mechanical in nature. Numerical changes in chromosomes have been dealt with in Chapter X. There is yet another type of change which involves sections or whole chromosomes leading to different rearrangement of genes in the same chromosome or of sections in different chromosomes. According to the chromosome theory each species or race has a constant chromosome number, each chromosome has a definite gene complex and their linear order is fixed. These stable structural features of the nucleus constitute the *Karyotype* of the organism. If the chromosome structure undergoes a change, it may be reflected in the breeding behaviour of the organism. These intra-chromosomal changes have played a great part in the evolution of species. These changes may or may not involve modifications of chromosome morphology but they alter the hereditary characters of the organism and sometimes raise it to the level of new species or races.

Sometimes, these structural changes in chromosomes are loosely referred to as mutations.

2. **Types of structural changes.**-During the resting change of the nucleus, the chromosomes lie inside the nucleus like a tangle of threads. During prophase, chromosomes are the longest and slowly they disentangle themselves and prepare to arrange themselves for the second stage of cell division. In doing so, sometimes the chromosomes may break and the broken ends of chromosomes reunite giving rise to chromosomes with different gene arrangements. *The chromosomes exhibit the peculiar property of uniting at the broken ends only.* Two growing twigs of plants do not unite with each other when merely brought together; but in grafting such twigs, they are cut and the cut ends are placed in close contact to each other. Very soon the broken ends unite bringing about a new combination of the stock and scion. Analogous to the union of cut ends in grafting, the broken ends of chromosomes are found to be 'sticky'. If for any reason, chromosomes break and reunite differently at the broken ends, they cause new arrangement of genes and this in turn may be reflected in the breeding behaviour of the organisms.

It has been pointed out that the centromere is an important entity in the chromosome. When chromosomes break and reunite, the possibilities are that as a result of reunion (*a*) a fragment with centromere may unite with another fragment without centromere (*b*) a fragment with centromere may

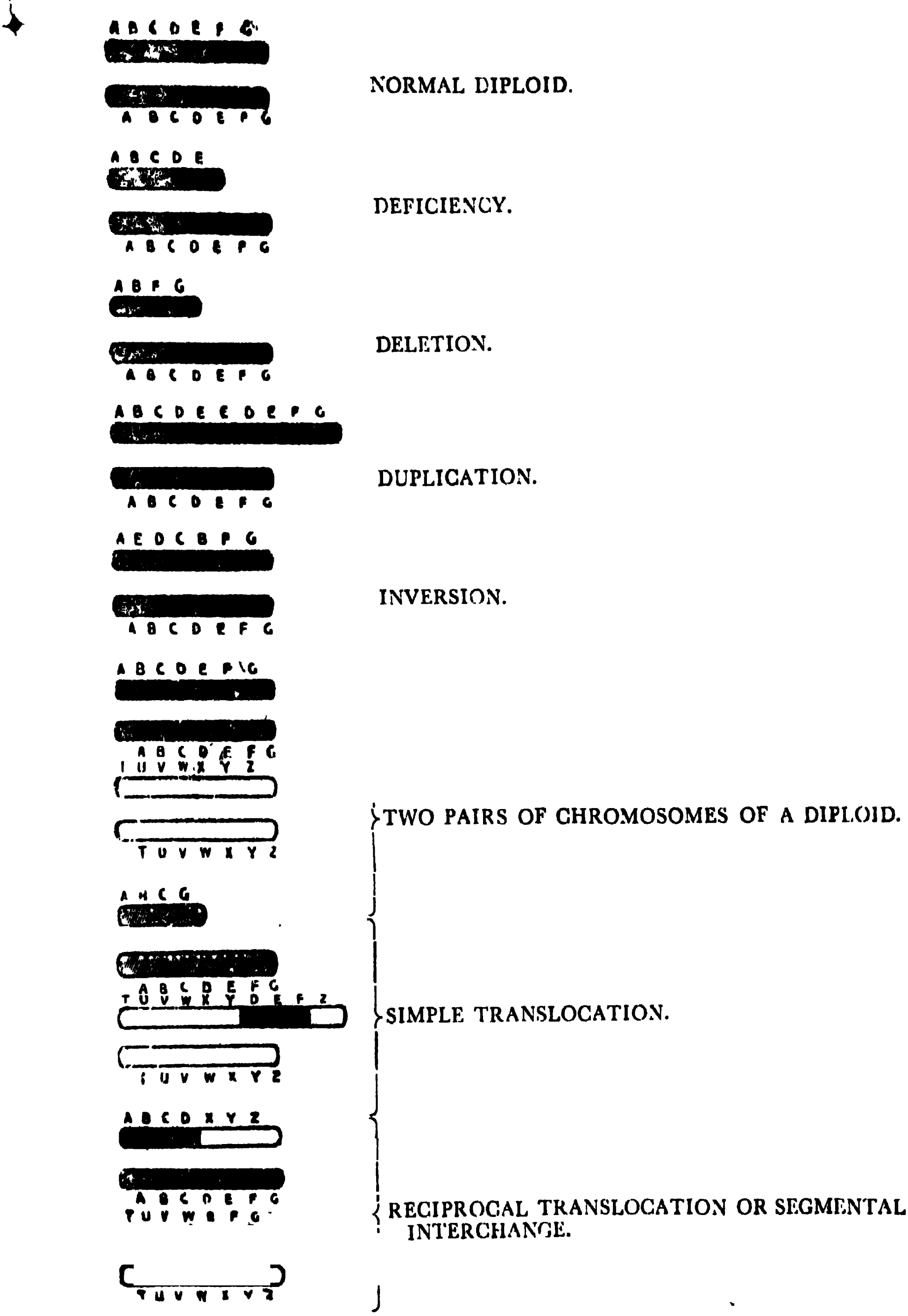


Fig. 94. To illustrate the types of structural changes in chromosomes.

unite with another centric fragment, (*c*) two noncentric fragments may unite. Only in (*a*) the resultant chromosome is functional and (*b*) and (*c*) are soon lost in ontogeny.

the chromosomes are 1. 2; 3. 4; 5. 6; 7. 8;...23.24—each pair of numbers shows the two ends of a chromosome. This weed has been inadvertently spread from place to place by man. The geographical races are morphologically alike but yet their chromosomes proved to be structurally different. Thus, the Peruvian and Chilean populations seemed to possess 1·18; 2·17; 11 21; 12·22. F_1 of a cross between these and the standard type showed two rings with four chromosomes each and 8 bivalents. Formation of rings of chromosomes has been observed in all the species mentioned in the preceding para. When homozygous for the translocation, the race breeds true. When a chromosome segment is translocated it naturally leads to a change in the linkage relationship.

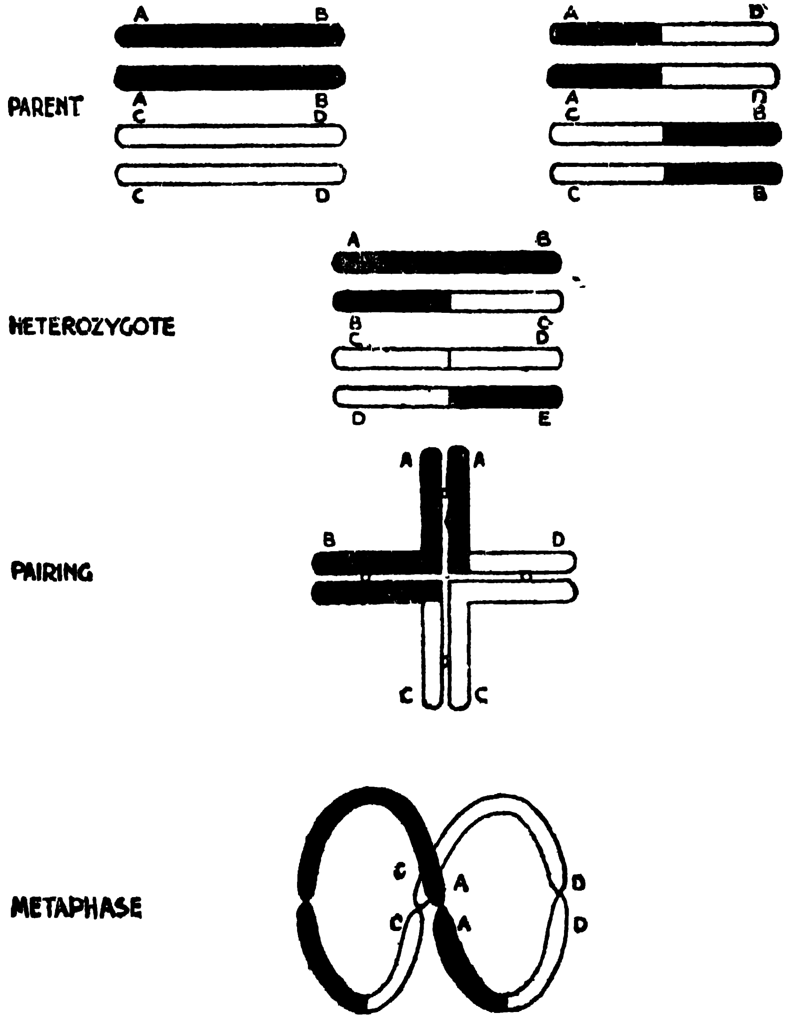


Fig. 95. To illustrate the formation of ring chromosomes in an interchange heterozygote.

A case of segmental interchange was noticed in the progeny of X-rayed seed of a pure line rice T. 24. The progeny was semi-sterile mutant and in almost all the pollen mother cells association of four chromosomes was noticed.

Semi-sterility and the association of four chromosomes result from segmental interchange or *illegitimate crossing over*. If two chromosomes AB.CD interchange segments B and D the interchanged chromosome will be AD.CB. The heterozygote will then be AB. BC and CD.DA. At meiosis while pairing, homologous segments come together and hence a ring of four chromosomes is formed. (Fig. 95).

Depending upon the number of interchanges in which the parents entering the cross differ, the ring formation will vary. If there are two interchanges, involving three non-homologous chromosomes, a ring of six chromosomes may be formed ; if the two interchanges are in two different sets of non-homologous chromosomes, two rings of four chromosomes each may be formed.

When a ring is formed, random assortment at anaphase results in the formation of 50% inviable gametes as explained below.

The *disjunction* of the ring AB. BC. CD DA. will result in two types of separation. (Fig. 95).

(1) AB.CD and BC.DA

or

(2) AB. BC and CD. DA.

In the first type, each gamete will contain all the four segments (A.B.C.D.) while in the second type deficiency and duplication are evident, *e.g.* the gamete

Fig. 96. X-ray mutants in rice : normal, semi-sterile and dwarf. (*With the kind permission of Jl. Gen.*)

AB. BC is deficient in segment D and duplicated in segment B. This gamete is inviable. For this reason the interchange heterozygote is 50% sterile.

Counts in diakinesis configurations showed that out of 100 cells, 16 showed rings or chains of 4 chromosomes and the rest showed different configurations with interstitial chiasmata. Failure of chiasmata at one end gives a configuration of neck-tie ($\propto$), while chiasmata at both ends give a figure of eight (8).

Formation of two types of gametes results in the obtaining of the following genotypes on selfing the semi-sterile plant.

(1) AB, AB. CDCD, which are like the normal plants.

(2) ABBC. CDDA which are heterozygous.

(3) BCBC. DADA which are dwarfs in this case. (Fig. 96.)

These three genotypes appeared in the ratio 1 : 2 : 1 in rice. Only in such rare instances, (1) and (3) may be morphologically distinguishable, but on crossing the hybrid will show chromosome ring and semi-sterility.

7. **Inversion.**—If there is reversal of the linear arrangement of genes in a segment without change in the total gene content, it is termed *inversion.* In a chromosome *ABCDEFG* inversion of the segment *BCDE* will change the chromosome to *AEDCBFG.* In such inverted segment the centromere may also be included or not. A second inversion may take place inside the first inversion and it is then termed *included inversion.*

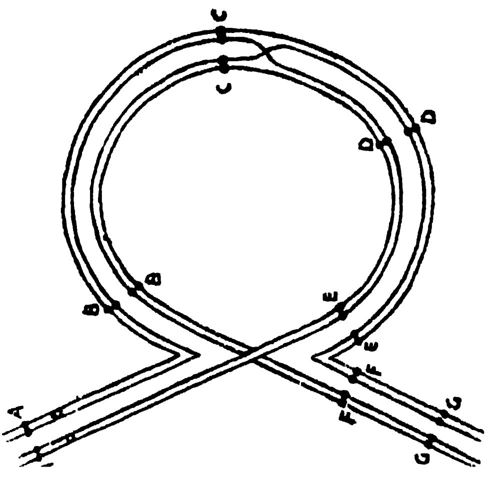


Fig. 97. Pairing of chromosomes in an inversion heterozygote.

The genetic consequence of inversion is suppression of crossing-over. This method of detecting inversion can be adopted only in cases where genetic analysis of the organism is complete and chromosome maps have been prepared. In *Diptera* inversion can be directly observed in the banding of salivary gland chromosomes. In heterozygotes for inversion, the inverted segment forms a loop to bring the homologous parts opposite to each other for pairing. (Fig. 97.)

A simple cross-over within the loops will lead to the formation of four types of chromatids, two resembling the parental ones, one with two centromeres (dicentric) and one without a centromere (acentric). The latter two are

abnormal and do not function. The acentric chromosome has no power of movement during cell division and hence lags as a fragment in the centre of the cell. The dicentric chromatid has two centromeres which pull the chromatids in opposite directions and the whole chromatin is stretched between the two poles forming a *chromatin bridge.*

Formation of chromatin bridge and a fragment at meiosis indicates that the organism is an inversion heterozygote. Chromatin bridges may not be evident in cases where crossing-over fails in the inverted segment if such a section is small. Therefore, non-appearance of chromatin bridge is no proof for the absence of inversion.

8. Evolutionary significance.—The consequences of these changes are important in evolution. *Structural changes bring about new genic interactions within the genotype and consequently the interaction with the environment also changes.* This may or may not involve visible changes in the morphology or physiology of the organism. The plant that has suffered structural change in its chromosome stands on a new footing in relation to the environment and also to its progenitor.

Homozygous deletions prove lethal to the organism. In the case of duplications, the genes in the 'repeats' may mutate differently from their formerly identical genes. In course of time, the derived progeny will have more kinds of genes than its progenitor. This is an important step in evolution.

Duplication by the addition of a centric fragment and translocation of other fragments on to this will cause an increase in the chromosome number of the individual. Similarly, deletion of a centric fragment may lead to a decrease in the chromosome number. Dubinin (1934, 1936) succeeded in producing *Drosophila* strains with three pairs or five pairs of chromosomes while the normal type possesses four pairs. The frequency of chromosomal changes in various races of organism is evidenced by the occurrence of unequal bivalents, chromosome morphological differences and differing chromosome numbers in a species.

That inversions play a role in speciation is shown from the fact that the races A and B in *Drosophila pseudo-obscura* differ from each other in four inverted sections. The gene arrangement may be different even within the same species.

Formation of rings and chains of chromosomes has been observed in many interspecific hybrids. It has been pointed out that a ring of four chromosomes brings about semi-sterility. Therefore partial or complete sterility by ring chromosomes may result from segmental interchange. Cross-sterility is a form of *genetic isolation.* The types which differ by segmental interchange cannot cross and establish varying intergrades. The types take different paths in their evolution on account of genetic isolation brought about by segmental interchange.

Chapter 12

EVOLUTION AND NATURAL SELECTION

EVOLUTION — SPECIES FORMATION — GENETIC ANALYSIS — NATURAL SELECTION — ORIGIN OF CULTIVATED PLANTS — SPECIES DIFFERENCES

1. **Evolution.**—Organisms change in course of time. Though the change is not large and perceptible from generation to generation new species are evolved from old species which may also exist or become slowly extinct. Evidences for this are from many sources, chief of which may be mentioned Palaeontology. Fossil studies show that only few species existed in the earliest of geological ages and that by passage of time there appeared diverse forms and new species.

It is the study of evolution which interested many workers in problems relating to variation. Without variation new species cannot arise. Theories of Lamarck and Darwin have been already discussed. After the re-publication of Mendel's work a real knowledge of the mechanism of variation was available. Mendelian heredity was studied in a very large number of plants with a view to understand the causes of variation and trend of evolution.

Classification of diverse forms is the first step to understand the trend of variation. Various systems were devised based on morphological differences of which *the Linnean conception of the species is still accepted as the workable basis from a taxonomist's view*. However, extensive studies in recent times, especially based on genetic studies of diverse forms and a survey of world collections of species show that the Linnean conception of species as typified by the herbarium specimens is far from indicating the variation that is really existent in the field and also the classification does not give a real insight into the changes involved in the formation of new species. *Therefore, a Linnean species is but a node in the continuous variation observed in Nature.* Genetic studies show that the small variations observed within the species, which are probably not of any significance to an old taxonomist are also important in nature.

Systematics or classification of organisms on taxonomical scale is the basis for the study of evolution. This branch of science was of narrow significance some three decades ago but now cytogenetic, developmental, physiological ecological and palaeontological studies combined with field natural history and selection theories based on mathematical deductions have given a wider scope for the understanding of the differentiation of species. The problem of evolution is therefore to be solved by the study of variations in the field. Unlike in the nineteenth century, study of variation to-day is based on genetic studies subject to mathematical analyses. Darwin laid emphasis on the importance of selection in evolution and this is confirmed in a modified form by recent genetical studies. Selection varies in intensity and direction with the population density and varying ecological conditions.

In the case of crop plants, a study of variations existing in nature not only within the species but also in the allied species and genera of different geographical centres is now found to be helpful in two ways (1) *it may be possible to find in nature a form which is most suited for introduction into cultivation as an improved type* (2) *the evolutionary changes in different places have progressed in different directions and therefore it is possible to find useful genotypes either within the same species or in the allied species and ancestral forms.* These types may be used in the hybridisation programme with a view to transfer the required genotype in the local cultivated form. This problem is further discussed in a later chapter.

2. Species formation.—According to Darwin, variety is an incipient species. Gradual accumulation of differences leads to formation of new species. Genetic differences form the basis for species formation and classification. Hurst defines species as "*group of individuals of common descent with certain constant specific characters in common which are represented in the nucleus of the cell by constant and characteristic sets of chromosomes carrying homologous specific genes causing intra fertility and inter-sterility*". On this basis there may be two species which are morphologically identical but yet may be considerably different on genetic bases, *e.g.* the two races A and B of *Drosophila pseudo-obscura* are morphologically indistinguishable but they are inter sterile due to inversions in the chromosomes. But to rank them in two different species involves practical difficulties in that their identification is impossible without crossing them. The initial small differences in chromosomal structure, such as inversions, segmental interchanges etc. form the basis of genetic isolation between the group of organisms. To start with, these groups may be morphologically identical as in A and B races of *Dipseudo-obscura* but soon they become more and more divergent due to genetic isolation by inter-sterility. It is impossible for the two groups to cross and establish intermediate forms through recombination. *When such genetic isolation is established for any reason to be discussed hereafter, further changes in the genic content may proceed in different directions leading to the formation of distinct species.*

The same effect may be brought about by *geographic isolation*. When a group of organisms is isolated by geographical barriers such as mountains, rivers, etc., natural hybridisation between the groups is impossible and therefore changes in genetic constitution may proceed in different directions in the isolated forms. In course of time the divergence between them becomes greater and greater and this leads to the formation of distinct species.

In the absence of geographical barriers to isolate the groups other causes may split large population. For example, if a mutation for heterostyly or self-sterility occurs, the mutant will diverge from self-fertile group. If, in a group, time of flowering is considerably changed intercrossing becomes difficult and it creates conditions favourable for species differentiation. In species differentiation, not only morphological differences are to be considered but also geographical, genetical and ecological distinctness combined with incompatibility or sterility of the hybrid are to be taken into account,

If a naturally existing population is split up into groups at random by any natural barriers, such as their distribution in different islands, the population starts with initial differences among themselves and proceeds to differentiate further, probably in different directions. In such cases, the diversification is much greater than what would have been the case if the population had been growing in vast continuous stretch without forming groups by barriers. This type of variation is termed *Sewall-Wright effect.* Such speciation has been studied in great detail in the case of snails.

There are some species which are spread in wide areas and there are others that are confined to small areas *i.e., endemic species.* On the hypothesis of Darwin, the endemic species are relics of species which are becoming extinct and are existent in small areas where conditions specially favour them.

Willis' (1922) hypothesis holds that it is probable that endemic species may be considered as a new species that has just originated but has had no time to spread on large areas. *Age of the species is an important factor in the area it occupies under natural spread.* There is another suggestion by Willis in regard to speciation, *viz.*, that a new genus would start with a single species and later more species would be developed. Therefore monotypic genera are the youngest.

There are thus two assumptions regarding origin of species (1) Darwinian principle of gradual evolution (2) Sudden origin and later spread according to Willis. Both these hypotheses have not taken genetical factors into consideration. At present, the correct approach to origin of species, is a consideration of genetic factors in combination with selection.

3. **Genetic analysis.**—In the preceding chapters it was emphasised that genetics is a study of heredity and variation. Therefore the resemblance or differences between species must be explicable on genetic basis. Fluctuating or developmental variation arising out of environmental conditions are not heritable and therefore they do not play any role in evolution. The variations in the genotype have been already discussed and their role in evolution may again be summarised.

The following groups of genotypic variations have been discussed in the preceding chapters.

(1) Gene mutations.

(2) Changes in chromosome number—polyploidy and aneuploidy.

(3) Inter-chromosomal variations—translocation, interchange, inversion, deletion and duplication.

(4) Recombination through hybridisation.

New forms may arise by gene mutations unaccompanied by any other type of chromosomal aberration. In the case of crops such as *Lathyrus odoratus* tomato, peach, etc. a large number of varieties have arisen by gene mutation. In such cases, continued selfing, selection and preservation of mutant forms were responsible for the existence of numerous varieties in them. In some cases the morphological variations are large enough to deserve sub-specific

status. Thus, in the case of groundnut, the spreading and bunch types in one cross proved to be complementary. Similarly *Oenothera brevistylis* shows monogenic difference with *O. lamarckiana*. In many cultivated crops, mutation established large differences.

Variations arising out of changes in chromosome number have been discussed in Chapter X. Even within the same species, the chromosome number may be different and this might have arisen to enable the plant to adapt itself to the environment. This has been pointed out in the case of *Saccharum spontaneum* whose chromosome number is different in different localities. Many species have arisen by polyploidy. The case of related wild species allied to potato is shown below to indicate polyploidy.

2n—24 chromosomes group.—

Solanum ajanhuiri.

S. bukasovii.

S. vavilovii.

2n—36 chromosomes group.—

S. juzepczukii.

S. medians.

2n—48 chromosomes group.—

S. acaule.

S. ajuscoense.

S. andigenum.

S. antipoviczii.

S. edinense.

S. tuberosum.

2n—60 chromosomes group.—

S. curtilobum.

S. semidemissum.

2n—72 chromosomes group.—

S. demissum.

Formation of new species by allopolyploidy was also discussed in Chapter X. *Brassica juncea* is an amphidiploid from the cross *B. campestris* × *B. nigra*. The upland American cottons such as Cambodia are allopolyploids from a cross between 13 chromosomes Asiatic cotton (probably *G. arboreum*) and another New World cotton (probably *G. raimondii*).

Intra chromosomal differences are also important as initial steps in the evolution of new species. These differences may or may not be accompanied by morphological differences. Thus the European and Himalayan races of pea show no large morphological differences but the hybrid between them is

semi-sterile due to segmental interchange. In studying the hybrid between K_2 (*G. arboreum*) × *G. stocksii* it was found that only seven chromosomes of *G. stocksii* have homologous in the other species of old world cottons and the remaining six chromosomes might have had different origin. Thus the chromosomal variations provide the basis for variations and evolution of new species.

4. **Natural selection.**—Among the many variations provided by the above mentioned processes only a few of them are favoured in nature and they survive. This survival of the fittest type is what is termed as *Natural Selection*. To start with, even though continuous variation may be present within the population, selection of a few fitting types and the elimination of a large number of variants occur. Thus, the original population is split up into groups with larger differences between them and the continuity of variation within the population is broken here and there. The continued operation of natural selection isolates small divergent populations which in turn hastens divergence between the groups and formation of new species. *In nature, a stable species is therefore an end product of evolutionary changes.* From fewer and fewer ancestors in the remote past, diverse species have been derived. It is to be considered whether the changes in the plant are for the better and whether there are structural or physiological advantages in the new type over the ancestral type.

Most of the mutant forms are recessive to normal. The mutant forms are rarely advantageous over the wild ones because the change in most cases has been deleterious. Therefore, most of the mutant forms survive only under cultivation or preservation by man. *Thus the cultivated plants are characterised by a large number of recessive genes which arose by mutation and the progenitors of cultivated forms are characterised by wild type or dominant genes.*

When variations have arisen due to any of the genetic phenomena, selection comes into operation. Darwin's theory of evolution was based on "*competition*" and "*survival of the fittest*". *Natural selection does not in any way direct the variations in the organisms, but it operates on the variations when they arise.* The changes are not in any way directive or purposive. Natural selection acts as a sieve to select some and extinguish others. If it were to direct the changes in the organisms, the latter will be most adapted to the environment and any sudden change in the environment will make the organism unsuitable to the changed condition and then it will become extinct. Lamarck explains evolution on the basis of directive influence of environment on the change in the organism but this view is no more accepted. (Fig. 98).

Chance variations occur in nature and their survival in the organism is decided by the advantages it confers to it and this is referred to as *selection advantage* or *survival value*. This is decided by various factors such as protective colouration or mimicry, physiological conditions to suit soil or climate, contrivances to multiply and maintain the race against destructive forces, etc.

Survival on the basis of competition as conceived by Darwin laid emphasis on the enormous reproducing capacity of the organism in relation to the

population that survived. He did not explain the adaptation in the surviving population. Thus tobacco and *Argemone mexicana* produce thousands of seeds. If all seeds from all the plants survive the limited space on earth will not be sufficient even for one species. Only a few of the progenies survive due to the operation of *Natural selection*. The continued operation of Natural selection results in the *Evolution* of new species. Variation in the population is the basis for the operation of Natural Selection and Evolution. The mechanism came to be recognised only after the rediscovery of Mendel's laws.

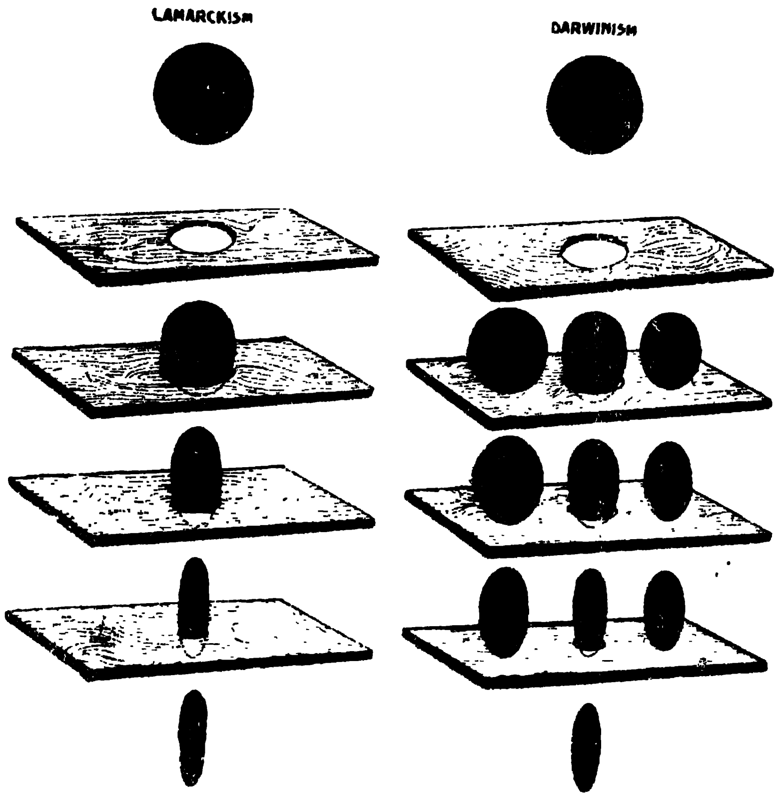


Fig. 98. Diagram to illustrate Lamarckism and Darwinism. Natural selection acts as a sieve. Note that in Lamarckism, natural selection has directive influence In Darwinism, variation in the progenies, competition and survival of the fittest play the role in evolution.

Darwin conceived heredity on blending type and not on particulate type. Mathematical deduction by Fisher shows that this type of inheritance will rapidly reduce variation and lead to extinction of the species. Change of place and climate are not considered to be potent causes for variations to arise. This has been recently proved by Vavilov who finds that *the greatest variability in any crop plant is in its restricted place of origin.* If natural selection is to continually operate on any population it is clear that there must be variability or potentiality for such variability.

Fisher, Wright and Haldane have mathematically dealt with the problem but yet no real insight in this problem of natural selection is available.

The problems connected with natural selection and evolution are of great importance to students of agriculture. The various crops which are now cultivated are also subjected to natural selection. Varieties of crop plants are variants which arose in nature and which are maintained by man for their economic value. If they are not cared for and preserved by man, under natural conditions they have no survival value. In modern agriculture, plant breeders are constantly at selection work and improved strains are released for large scale cultivation. The breeders test the strains for short periods only and their tests mainly concern the yielding capacity and economic qualities. The selected strains are selfed and maintained pure and thus variability in the population is reduced to the minimum level. Therefore the field for the operation of natural selection is much restricted in the breeders' material which is maintained pure artificially. Under natural conditions these strains may change and deteriorate.

That Natural Selection operates even on variability present in cultivated crops is shown by mixture experiments. Harlan and Martini (1938) reported on one such experiment. Eleven varieties of barley were raised at ten agricultural stations for a period of 4 to 12 years and the rate of natural selection in the mixture of varieties was studied. At all the stations, less adapted types were eliminated soon by the action of natural selection. The leading variety varied with the different localities. This aspect of the problems is further discussed in a latter chapter.

5. **Origin of cultivated plants.**—The earliest belief in regard to origin of cultivated plants is that such plants are gifts from God or that they are gradual transformations from the wild types in the course of cultivations in good soil and under good culture. Even until 1807 the origin of cultivated plants remained a mystery. The first scientist to gather evidences from varied sources was De Candolle.

De Candolle (1883) studied 247 species of cultivated plants and speculated their origin based on a variety of evidence. The works of ancient historians like Theophrastus, Chinese writings, archaeological findings such as Egyptian monuments, remains of Pompei and the remains of Swiss lake dwellings, philological evidences from the names of crops in different languages and botanical evidences based on the number of variations and distribution are some of the evidences on which he based his conclusions. He grouped the cultivated plants as follows :

Old World species cultivated for over 4000 *years.*

Almond.	Cabbage.	Millet.	Rice.
Apple.	Cucumber.	Mulberry.	Sorghum.
Apricot.	Date.	Olive.	Soybean.
Banana.	Fig.	Onion.	Tea.
Barley.	Flax.	Peach.	Turnip.
Bean.	Grape.	Pear.	Water melon
Brinjal.	Hemp.	Quince.	Wheat.

Old World species cultivated for over 2000 years and perhaps longer.

Asparagus.	Chestnut.	Nutmeg.	Rye.
Alfalfa.	Cotton.	Oats.	Sugarcane
Beet.	Grape fruit.	Orange.	Walnut.
Bread fruit.	Lemon.	Pepper.	Yam.
Carrot.	Lettuce.	Plum.	
Celery.	Lime.	Poppy.	
Cherry.	Mustard.	Radish.	

Old World species cultivated probably for less than 2000 years.

Artichoke.	Endive.	Okra.	Rhubarb.
Buckwheat.	Gooseberry.	Parsley.	Strawberry.
Coffee.	Horse radish.	Parsnip.	
Currant.	Muskmelon.	Raspberry.	

New World species of ancient cultivation more than 2000 years.

Cocoa.	Maize.	Tobacco.
Kidney bean.	Sweet potato.	

New World species cultivated before the time of Columbus : antiquity not known.

Avocado.	Peanut	Chilli.
Cotton	Pineapple.	Squash.
Guava.	Potato.	Tomato.
Jerusalem artichoke.	Pumpkin	Vanilla.

New World species cultivated since the time of Columbus.

Allspice.	Cinchona.	Plum.
Blackberry.	Cranberry.	Rubber.
Blackwalnut.	Dewberry.	Strawberry.
Blue berry.	Persimmon.	

Out of the 247 species studied by De Candolle, only 26 cultivated forms did not show wild progenitors. Probably the latter died out. That the cultivated plants originated in few places is shown by the fact that Swiss lake dwellings, a region inhabited by civilised man thousands of years ago, show cultivated types of plants whereas Australia which is invaded by man only in recent times entirely lacks such forms.

Darwin (1868) considered that the cultivated plants arose by profound modifications in the wild plants under cultivation. But he could not explain how these modifications were brought about in nature or under cultivation, as it was by then known that acquired characters are not inherited.

The work of Mendel brought to light the laws of inheritance. Mendel himself was of opinion that variations in nature are due to hybridisation and selection.

Vavilov (1926, 1935) made extensive collections of cultivated forms and their wild allies by sending expeditions to the various parts of the world. In tracing variations from different parts of the world Vavilov found wide diversities in certain regions. In some cases such as Abyssinia for wheat and South America for potato, more than half the diversity found in the whole world was present in these regions alone. *Such regions are few only in number and*

they are generally the small territories concentrated in mountains or foot hills in tropics and sub-tropics. Vavilov considers these as *primary centres* of origin for cultivated crops, *i.e.*, all the cultivated crops of the world had their origin in these centres and later they spread to different places of cultivation. These primary centres are rich in wild species of the cultivated forms and also in varietal forms and other diversities. All grades of variations from cultivated type to a perfectly wild species are to be found here. Thus, in the case of potato a search in its primary centre of origin, viz., Andean countries, shows all grades of variation from a perfectly tuber forming cultivated type to the wild non-tuber forming types. *These centres are predominated by dominant genes unlike in the case of parts of the world with cultivated forms only in which latter, recessive genes are to be found in large numbers.* Thus a definite route by which the wild types were transported to different parts of the world in the course of cultivation can be established by genetic studies. In the course of cultivation various mutants arose and these mutations being recessive could be preserved under cultivation only. Man found uses for these mutants and hence preserved them under cultivation. Therefore, the wild forms are characterised by dominant genes while the cultivated ones are characterised by recessive genes. This is shown in the following example of a cross between wild and cultivated rice.

TABLE 50.

Character.	Wild.	Cultivated.	F_1.
Leaf sheath ...	Purple ..	Green ..	Purple.
Pulvinus ...	Light purple ..	White green .	Light purple.
Ligule	Do. .	Do .	Do.
Margin of leaf ...	Purple ..	Green .	Purple.
Auricle ...	White green .	White green ..	White green.
Node ...	Purple	Green ..	Purple
Internode ...	Do. .	Yellow green .	Do.
Outer Glume ...	White green ...	White green .	White green.
Inner glume ...	Green with black tinge ultimately black.	Green	Green with black tinge ultimately black.
Apiculus ...	Light purple ...	White green ...	Light purple.
Awn	Awned long ...	Trace and short ...	Awned long.
Stigma ...	Deep purple ...	White	Deep purple.
Straw ...	Weak (spread) ...	Strong (erect) ...	Weak (spread).
Panicle	Spreading ...	Close	Spreading.
Inner glume ...	Black	Yellow	Black.
Kernel (pericarp) ...	Red	White	Red.

Based on the varietal and species diversity, Vavilov postulates eleven primary centres of origin for the cultivated crops (Fig. 99).

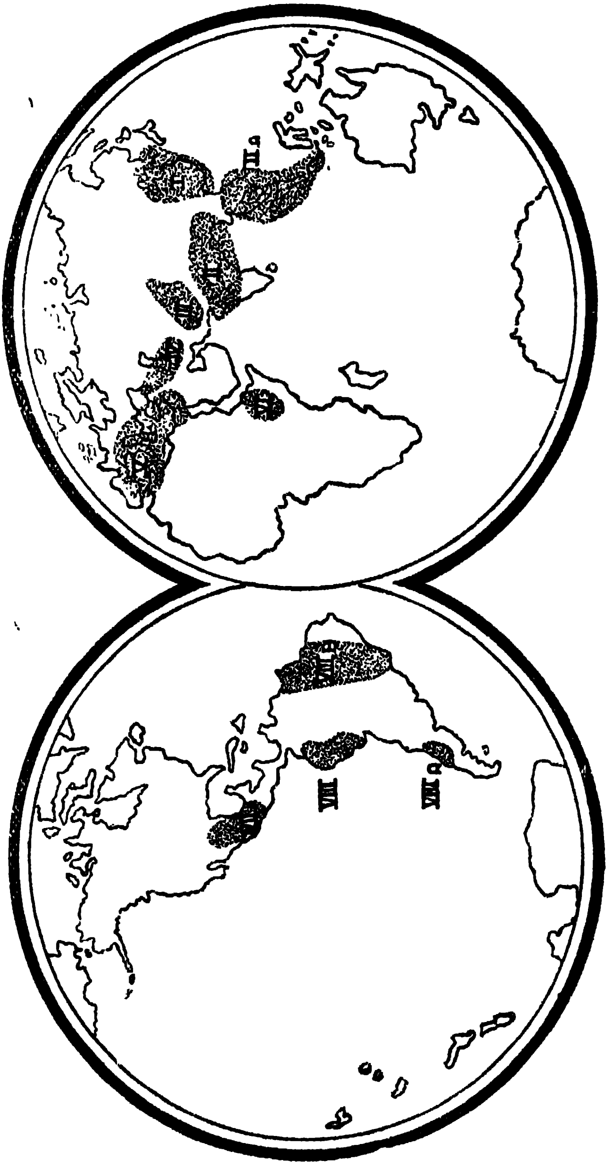


Fig. 99. Primary centres of origin for cultivated plants.

I. The Chinese centre of origin of cultivated plants :–

The earliest and the largest independent centre of the worlds agriculture and of the origin of cultivated plants consists of the mountainous regions of the central and western China.

1. *Panicum miliaceum.* L.,—Broom Corn Millet.
2. *P. italicum.* L.,—Italian Millet.

3. *P. frumentaceum*—Fr. and Sar. Japanese barnyard millet.
4. *Andropogon sorghum*—Brot Kaoliang.
5. *Avena nuda*. L.,—Naked Oats.
6. A group of endemic hull less awnless barley varieties (*Hordeum hexastictum, L.*)
7. Groups of Waxy Maize varieties.—*Zea mays*.—L., (Secondary centre).
8. *Fagopyrum esculentum*. Mœnch.—Buck wheat.
9. *Glycine hispida*. Maxim.--Soya Bean.
10. *Phaseolus angularis*. Wight.—Adzuki Bean.
11. *Phaseolus vulgaris*. L.,—Bean (secondary centre).
12. *Vigna sinensis*. Endl.--Subsp. *Sesquipedalis*.—Cowpea (secondary centre).
13. *Phyllostachys tuberula*. Munro, and other species.
14. *Dioscorea batatas*. Decne. Chinese Yam.
15. *Raphanus sativus*. L.,—Radish.
16. *Brassica rapa*. L.,—Turnips.
17. *Nelumbo nucifera*. Goertn.—Lotus.
18. *Sagitaria sagittifolia*. L.,—Arrowhead.
19. *Trapa bispinosa*. Roxb.—Water Chestnut.
20. *Brassica chinensis*. L.,—Pak Choe.
21. *B. juncea*. Czern.—Leaf mustard.

    (Secondary centre of origin).
22. *Allium fistulosum*. L.,—Spanish Onion.
23. *Lactuca sp.*—Stem Lettuce.
24. *Solanum melongena*. L.,—Eggplant.
25. *Cucumis sativus*. L.,—Cucumber.
26. *Cucurbita moschata*. Var *Toonasa*.—Makino., warty squash (secondary centre).
27. *Chrysanthemum coronarium*. L.,—Chrysanthemum.
28. *Basella cordifolia*. Lam.—Chinese Spinach.
29. *Pyrus serotina*. Rehd.—Chinese Pear.
30. *Malus asiatica*. Nakai.—Chinèse Apple.
31. *Prunus persica*. L.,—Peach.
32. *P. armeniaca*. L.,—Apricot.
33. *Zizyphus sativa*. Gaertn.—Chinese jujube.
34. *Juglans sinensis*. Dode.—Walnut.
35. *Citrus sinensis*. Osb.—Orange (secondary centre).
36. *C. nobilis*. Lour.
37. *Diospyros kaki*. L.,—Persimmon.
38. *Litchi chinensis*. Sonu.—Litchi.
39. *Saccharum sinense*. Roxb.—Endemic group of Sugarcane varieties.
40. *Aleurites montana*. Wilson.—Wood oil tree.
41. *Melia azadirach*. L.,—China Berry.
42. *Sesamum indicum*. L.,—Sesame (Secondary centre).
43. *Cinnamomum cassia*. L.,—Chinese Cinnamon.
44. *Camellia sinensis*. L.,—Tea.
45. *Papaver somniferum*. L.,—Opium poppy.
46. *Aconitum wilsonii*. Hort.—Aconite.

47. *Bohemeria nivea.* Hook and Arn.—Ramie.
48. *Trachycarpus excelsus.* Makino.—Fibre Palm.
49. *Metroxylon sagu.* Rottb.
50. *Cycas revoluta.* Thunb.—Sagopalm.

II. The Indian centre of origin of cultivated plants (exclusive of North West India, Punjab, including Assam and Burma).

1. *Oryza sativa.* L.,—Rice.
2. *Andropogon sorghum.* Brot.—Sorghum.
3. *Eleusine coracana.* Gaertn.—African Millet.
4. *Paspalum scrobiculatum.* L.
5. *Cicer arietinum.* L.,—Chickpea.
6. *Cajanus indicus.* Spreng.--Pigeonpea.
7. *Phaseolus aconitifolius.* Jack.—Mat bean.
8. *P. mungo.* L.,—Black Gram.
9. *P. aureus.* (Roxb).—Mung Bean.
10. *Dolichos biflorus.* L.
11. *D. lablab.* L.,—Hyacinth Bean.
12. *Vigna sinensis.* Endl.—Cowpea.
13. *Trigonella foenum graecum.* L.,—Fenugreek.
14. *Canavalia gladiata.* D. C.—Sword Bean.
15. *Cyamopsis psoralioides.* D. C.—Guar.
16. *Amarantus speciosus.* Sims.—Amaranth.
17. *A. gangeticus.* L.
18. *Solanum melongena.* L.,—Egg Plant.
19. *Momordica charantia.* L.,—Bitter Gourd.
20. *Cucumis sativus.* L.,—Cucumber.
21. *Lagenaria vulgaris.* Ser.—Bottle Gourd.
22. *Luffa acutangula.* Roxb.—Ribbed Gourd.
23. *Trichosanthes anguina.* L.,—Snake Gourd.
24. *Lactuca indica.* L.,—Indian Lettuce.
25. *Colocasia antiquorum.* Schott.
26. *Dioscorea alata.* L.,—Yam.
27. *Amorphophallus campanulatus.* Blume.—Elephant Yam.
28. *Mangifera indica.* L.,—Mango.
29. *Citrus sinensis.* Osb.—Orange.
30. *C. nobilis.* Lour.
31. *C. limonia.* Osb.—Lemon.
32. *C. medica.* L.,—Citron.
33. *C. aurantium.* L.,—Sour Orange.
34. *C. aurantifolia.* L.,—Sour Lime.
35. *Phoenix silvestris.* Roxb.—Wild Date.
36. *Mimusops elengi.* L.
37. *Feronia elephantum.* Correa.—Wood apple.
38. *Eugenia jambolana.* Lam.—Jambo.
39. *Artocarpus integra.* Merr.—Jack Fruit.
40. *Aegle marmelos.* Correa.
41. *Averrhoa bilimbi.* L.,—Bilimbi.
42. *Carissa carandas.* L.

43. *Phyllanthus emblica*. L.,—Myrobalan.
44. *Murraya keonigii*. Ser.
45. *Tamarindus indica*. L.,—Tamarind.
46. *Saccharum officinarum*. L.,—Sugarcane.
47. *Arenga saccharifera*. Labill.—Sugar Palm.
48. *Cocos nucifera*. L.,—Cocoanut Palm.
49. *Sesamum indicum*. L.—Sesame.
50. *Carthamus tinctorius*. L.,—Safflower.
51. *Brassica juncea*. Czern.—(Possibly secondary centre of origin).
52. *B. nigra*. Czern.—Black mustard.
53. *Gossypium arboreum*. L.
54. *G. obtusifolium*. Roxb.
55. *Corchorus capsularis*. L. } Jute.
56. *C. olitorius*. L. }
57. *Crotalaria juncea*. L.,—Sunnhemp.
58. *Sesbania aculeata*. L.
59. *Hibiscus cannabinus*. L.
60. *H. sabdariffa*. Roselle.
61. *Bombax malabaricum*. DC.
62. *Cannabis indica*. L.,—Hemp.
63. *Piper nigrum*. L.,—Black Pepper.
64. *P. betle*. L.,—*P. Longum*. L.,—Betlenut.
65. *Elettaria cardamomum*. Maton and White.—Cardamon.
66. *Areca catechu*. L.
67. *Cuminum cyminum*. L.,—Cumin.
68. *Acacia arabica*. Willd.—Gum Arabic.
69. *A. catechu*. Willd.
70. *Cymbopogon nardus*. Rendle.—Citronella Grass.
71. *Santalum album*. L.,—Sandalwood.
72. *Indigofera tinctoria*. L.,—Indigo.
73. *Rubia tinctorum*. Madder.
74. *Lawsonia alba*. Lam.—Henna.
75. *Terminalia catappa*. L.,—Indian almond.
76. *Cassia angustifolia*. Vahl.—Senna.
77. *Cinnamomum zeylanicum*. Breyn.—Cinnamon.

II-A. The Indo-Malayan Centre of origin of cultivated plants. This includes the entire Malay Archipelago and the large islands such as Java, Borneo, Sumatra, the Philippines and Indo-China.

1. *Dendrocalamus asper*.—Backer. Giant Bamboo.
2. *Dioscorea alata*. L.
3. *Zingiber officinale*. Rosc.—Ginger.
4. *Citrus microcarpa*. Bge.
5. *C. grandis*. Osb.—Pumelo.
6. *Coleus tuberosus*. Benth.
7. *Areca catechu*. L.
8. *Musa paradisiaca*. L.
9. *M. sapientum*. L.,—Banana.

10. *Garcinia mangostana.* L.,—Mangosteen.
11. *Artocarpus communis.* Frost.—Breadfruit.
12. *Aleurites moluccana.* Willd.—Candlenut
13. *Vetiveria zizanioides.* Stapf.—Vetiver.
14. *Cocos nucifera.* L.,—Cocoanut.
15. *Saccharum officinarum.* L.,— Sugarcane.
16. *Elettaria cardamomum.* Maton and White.— Cardamon.
17. *Myristica fragrans.* Houtt.—Nutmeg.
18. *Piper nigrum.* L.,- Black Pepper.
19. *Musa textilis.* Nee. Manila hemp.
20. *Curcuma longa.* L., –Turmeric.

III. The Central Asiatic Centre of origin of cultivated plants. It includes North-West-India (Punjab, N.W.F. Province, Kashmir) Afghanistan, Soviet Republics of Tadjikistan and Uzbekistan and Western Tian-Shan.

1. *Triticum vulgare.* Vill. Common Wheat.
2. *T. compactum.* Host.- Club Wheat.
3. *T. sphaerococcum.* Perc.- Shot Wheat.
4. *Secale cereale.* L., Rye (Secondary Centre)
5. *Pisum sativum.* L., -Pea.
6. *Lens esculenta.* - Moench-Lentil.
7. *Vicià faba.* L.,--Beans
8. *Lathyrus sativus.* L.
9. *Cicer arietinum.* L., –Chick pea.
10. *Phaseolus aureus.* Roxb. -Mungbean.
11. *P. mungo.* L..–Blackgram.
12. *Brassica campestris.* Subsp. *Oleifera* Metzg.--Rape. (Secondary – Centre).
13. *B. juncea.* Czern.– Mustard.
14. *Linum usitatissimum.* L., --Flax (one of the centres of origin).
15. *Sesamum indicum.* L., Sesame. (one of the centres of origin)
16. *Coriandrum sativum.* L.,—Coriander (one of the centres of origin)
17. *Carum copticum.* Benth and Hook.
18. *Carthamus tinctorius.* L., –Safflower.
19. *Cannabis indica.* L.,- - Hemp.
20. *Gossypium herbaceum.* L.,- –Cotton.
21. *Cucumis melo.* L.,—(Secondary Centre).
22. *Lagenaria vulgaris.* Ser.--(Secondary Centre)
23. *Daucus carota.* L.,—Carrot.
24. *Brassica campestris.* L.,- -Subvar *Rapifera.* Turnip.
25. *Raphanus sativus.* L.,—Radish (one of the centres of origin).
26. *Allium cepa.* L.,--Onion.
27. *Allium sativum.* L.,—Garlic.
28. *Pistacia vera.* L.,—Pistachio.
29. *Prunus armeniaca.* L.,—Apricot.
30. *Pyrus communis.* L.,-–Pear.
31. *Amygdalus communis.* L.,-- Almond.
32. *Vitis vinifera.* L.,—Grape.

IV. The Near-Eastern Centre of origin of cultivated plants including the interior of Asia-Minor, the whole of Transcaucasia, Iran, and the high lands of Turkmenistan.

1. *Triticum monococcum.* L.,—Einkorn Wheat (($n = 14$).
2. *T. durum.* Subsp. *Aav.*—Durum Wheat ($n = 28$).
3. *T. turgidum.* L.,—Poulard Wheat ($n = 28$).
4. *T. vulgare.* Vill—($n = 42$).
5. *T. persicum.* Vall.—Persian Wheat ($n = 28$).
6. *T. timopheevii.* Zhuk—(n 28).
7. *Avena byzantina.* C. Koch.—Mediterranean oats.
8. *A. sativa.* L.,—Common oats. (Endemic Varieties as weeds.)
9. *Cicer arietinum.* Subsp.—*Pisiforme* G. Pop (Secondary Centre).
10. *Pisum sativum.* L.,—Pea (Secondary Centre).
11. *Trifolium resupinatum.* L.,—Persian Clover.
12. *Vicia sativa.* L.,—Crop Vetch.
13. *Linum usitatissinum.* L.,—Flax.
14. *Brassica campestris.* L.,—Subsp. *Oleifera.* (Secondary Centre).
15. *Pimpenella anisum.* L.,—Anise.
16. *Coriandrum sativum.* L.,—Coriander. (One of the Centres).
17. *Cucurbita pepo.* L.,—Pumpkin. (Greatest diversity in Asia Minor).
18. *Beta vulgaris.* L.,—Garden Beet.
19. *Ficus carica.* L.,—Fig.
20. *Pyrus communis.* L.,—Pear.
21. *Punica granatum.* L.,—Pomegranate.
22. *Juglans regia.* L.,—Walnut.
23. *Crocus sativus.* L.,—Saffron.

V. The Mediterranean Centre of origin of cultivated plants.

1. *Triticum durum.* Desf.—Durum Wheat.
2. *T. dicoccum.* Schrank.—(One of the Centres).
3. *T. polonicum.* L.,—Polish Wheat. (One of the Centres).
4. *T. spelta.* L.,—Spelta Wheat.
5. *Hordeum sativum.* Jess.—Coarse Barley. (Secondary Centre).
6. *Pisum sativum.* L.,—Pea.
7. *Lupinus albus.* L.,—Lupines.
8. *Cicer arietinum.* L.,—Chickpea.
9. *Trifolium alexandrinum.* L.,—Egyptian Clover.
10. *Linum usitatissimum.* L.,—Subsp. *Mediterranium.* Vav.—Flax.
11. *Sinapis alba.* L.,—White Mustard.
12. *Beta vulgaris.* L.,—Garden Beet.
13. *Brassica oleracea.* L.,—Cabbage.
14. *B. campestris.* L.,—Subv. *Rapifera* Metzg.—Turnip. (Basic Centre).
15. *Allium cepa.* L.,—Large Onion (Secondary Centre).
16. *A. sativum.* L.,—Garlic (Secondary Centre).
17. *A. porrum.* L.,—Leek.
18. *Cichorium intybus.* L.,—Chicory.
19. *Cuminum cyminum.* L.,—Cumin.
20. *Mentha piperita.* L.,—Peppermint.

VI. The Abyssinian Centre of origin.

1. *Triticum durum*. Subsp.—*Abyssinicum* Var. Abyssinian Hard Wheat.
2. *T. dicoccum*. Subsp.—*Abyssinicum* Stol. Emmer Wheat.
3. *T. polonicum*. L.,—Polish Wheat.
4. *Hordeum sativum*. Barley.
5. *Andropogon sorghum*. Link.
6. *Eleusine coracana*. Gaertn.—Finger millet.
7. *Pennisetum typhoides*. L.,—Pearl Millet.
8. *Cicer arietinum*.—L.
9. *Lens esculentus*. Moench.—Lentil.
10. *Dolichos lablab*. L.
11. *Linum usitatissimum*. L.,—Flax.
12. *Carthamus tinctorius*. L.,—Safflower.
13. *Sesamum indicum*. L.,—Sesame. (Basic Centre).
14. *Coffea arabica*. L.,—Coffee.
15. *Musa ensete*. J. F. Gmel.—Abyssinian Banana.
16. *Hibiscus esculentus*. L.,—Okra.

VII. The South Mexican and Central American Centre of origin including Antilles.

1. *Zea mays*. L.,—Corn.
2. *Phaseolus vulgaris*. L.,—Bean.
3. *P. lunatus*. L.,—Lima Bean.
4. *Canavalia ensiformis*. D.C.—Jackbean.
5. *Amarantus paniculatus*. L.
6. *Sechium edule*. Swartz.
7. *Ipomoea batatas*. Poiret.—Sweet Potato.
8. *Cucurbita moschata*. Duch.
9. *Maranta arundinacea*. L.,—Arrowroot.
10. *Capsicum annuum*. L.,—Chillies.
11. *Gossypium hirsutum*. L.,—Upland Cotton.
12. *Opuntia sp*.—Pricklypear.
13. *Anona squamosa*. L.,—*A. reticulata*.—L., *A. muricata*.—L.
14. *Achras sapota*. Miller.—Sapota.
15. *Carica papaya*. L.,—Papaya.
16. *Psidium guayava*. L.,—Guava.
17. *Anacardium occidentale*. L.,—Cashew.
18. *Theobroma cacao*. L.,—Cacao.
19. *Bixa orellana*. L.,—Annatto.
20. *Nicotiana rustica*. L.

VIII, South American (Peruvian—Ecuadorean, Bolivian) centre of origin.

1. *Solanum andigenum*. Guz et Buk.
2. Other endemic cultivated potatoes.
   Solanum cuencanum. Juz and Buck.—($n=24$).
   S. kesselbrenneri. Juz and Buck.—($n=24$).

S. *ajanhuiri*. Juz and Buk.—($n=24$).
S. *panciflorum*. Juz and Buk.—($n=24$).
S. *stenotomum*. Juz and Buk.—($n=24$).
S. *goniocalyx*. Juz and Buk.—($n=24$).
S. *rybinii*. Juz and Buk.—($n=24$).
S. *bayacense*. Juz and Buk.—($n=24$).
S. *juzepczukii*. Juz and Buk.—($n=36$).
S. *tenuifilamentum*. Juz and Buk.—($n=36$).
S. *mamilliferum*. Juz and Buk.—($n=36$).
S. *choclo*. Juz and Buk.—($n=36$).
S. *riobambense*. Juz and Buk.—($n=36$).
S. *curtilobum*. Juz and Buk.—($n=60$).

3. *Zea mays*. L.,—Starchy Maize. (Secondary Centre).
4. *Phaseolus lunatus*. —L.,· Limabean. (Secondary Centre).
5. *Lycopersicum esculentum*. Mill.
6. *L. peruvianum*. Mill.—Tomato.
7. *Cyphomandra betacea*. Sendtn.—Tree Tomato.
8. *Cucurbita maxima*. Duch.—Pumpkin.
9. *Capsicum frutescens*. L.
10. *Gossypium barbadense*. L.,—Egyptian Cotton.
11. *Cinchona succirubra*. Pav.—Quinine tree.
12. *Nicotiana tabacum*. L., - Tobacco.

VIII (*a*) The Chile Centre of origin.

1. *Solanum tuberosum*. L.,—Common potato.

VIII. (*b*) Brazilian—Paraguayan Centre.

1. *Manihot utilissima*. Pohl.- Tapioca.
2. *Arachis hypogaea*. L., Peanut.
3. *Theobroma cacao*. L.,—Secondary Centre.
4. *Hevea brasiliensis*. Mull.—Rubber tree.
5. *Anacardium occidentale*. L.,—Cashew.

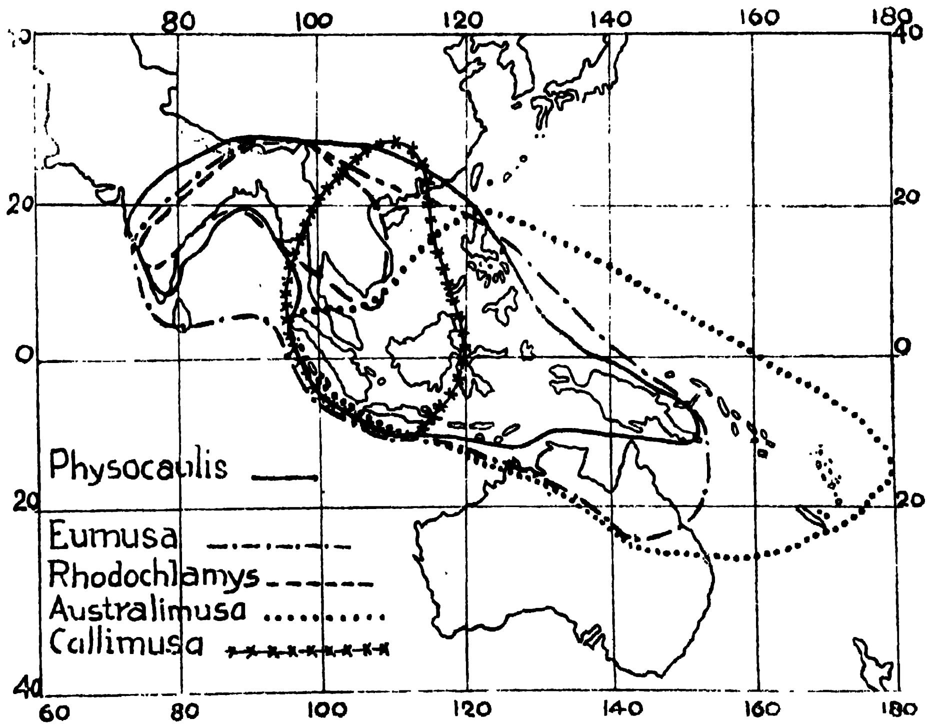
These regions are inferred to have been the most favourable for diversification and species formation. Such centres also represent the ancient localities of agricultural civilisation. The study of variations concentrated in these areas showed parallelism in morphology in different species which was later found to have had a genetical basis. *From these centres, the species have spread in different directions in the course of which many recessive mutations occurred.* Very rarely dominant mutations occurred as in the case of naked forms of oat barley and millet in eastern Asia which formed secondary centres of origin for these. In certain cases the trend of variation from the dominant forms of the primary centre to the recessive forms of the region where the species is under cultivation is traceable, though genetic analyses have not been carried out in all cases. Thus for example, the seeds of beans, lentils and chick peas show a gradual increase in size from the centre of origin in India to the cultivated regions of the Mediterranean. In many cases the cultivated forms in the centres of origin bear many dominant genes and are nearer to wild races than in the cases of the forms cultivated in the regions distant from these countries.

Ecological conditions have decided the forms most suitable to the places. Vavilov quotes an instance of flax where the early types were naturally selected in northern regions due to shorter vegetative period and these are cultivated there for fibre while the long duration types are cultivated in the south for oil. Cultivated crops have not arisen by a single phase or step but different steps might have resulted in a series of cultivated groups quite independent of the other. In many cultivated crops gigas forms have arisen by mutation or hybridisation. *Hybridisation enabled variations to arise not only by recombination but also by allopolyploidy.*

Origin of a few crop plants is discussed below :—

BANANA (*Musa Sp.*) De Candolle indicates Asiatic origin. The best cultivated forms are seedless and indicates to hybrid origin. Chakravorti (1951) postulates the origin of all the cultivated varieties and forms of bananas as descendants from two wild species of South-East Asia viz. *Musa acuminata* Colla., and *M. balbisiana* Colla., and their hybrids. These wild species are diploids ($2n=22$) while the edible types are triploids ($3n=33$). The triploidy is postulated to have arisen by union between reduced and unreduced gametes. The karyotypes of the triploids are variable due to spontaneous chromosome changes by deletion, inversion and translocation. Vegetative sports have also contributed to the numerous types under cultivation. Assam, Burma, Siam, Indo-China is postulated as centre of origin for all bananas.

Possibly no single hypothesis can explain the origin of the numerous cultivated types of bananas. (Vide Fig. 99-a :).



(*From Ind. Jl. Gen. & Pl. Br.*)

Fig. 99-*a*. Map showing distribution of different sections of *Musa* in South-East Asia.

BARLEY (*Hordeum vulgare*). The awned-hulled form has arisen in Abyssinia. The naked grains have originated in China and Eastern Himalayas. The two races are intersterile.

BRINJAL (*Solanum melongena*). It is a native of tropics of Old World. Chinese literature 1500 years old refers to it. According to Vavilov there are two centres of origin (1) sub tropical or tropical India (2) China.

Bahaduri (1951) postulates India as the first place of origin from where it later spread through Iran to North Africa including Egypt, Turkey and the Balkans. The cultivated types might have originated through parallel evolution.

CITRUS (*Citrus sp.*). Cultivated in the orient for thousands of years. North East India, Southern China and Cochin China are probable places of origin. Shaddock which is introduced from Java is wild in eastern Himalayas and Burma. *C. sinensis* which has been introduced into cultivation from Malta and Mozambique is found wild in Assam. Seville oranges are wild in India. So also many species of Aerumen. Except for Osmocitrus, Eastern India is the home for citrus varieties. *C. latifes* which is the primitive type is found in Assam. North East India shows the largest variations while the imported types are all without any variation.

COTTON (*Gossypium sp.*). American and Asiatic cottons have come into cultivation independently. There are no wild cottons in China. *G. arboreum* has its home in Africa, *G. herbaceum* in India and the American types in Central America.

GINGELLY (*Sesamum orientale*). De Candolle thought it to have originated from the Sunda isles. Hiltebrandt (1932) regarded Africa as primary centre of origin due to the presence of diverse wild species in this area. The cultivated species originating in this region reached Abyssinia and later India. India is the secondary centre of origin and the other secondary centre being Japan.

GROUNDNUT (*Arachis hypogoea*). This is never wild. There are ten species under the same genus.

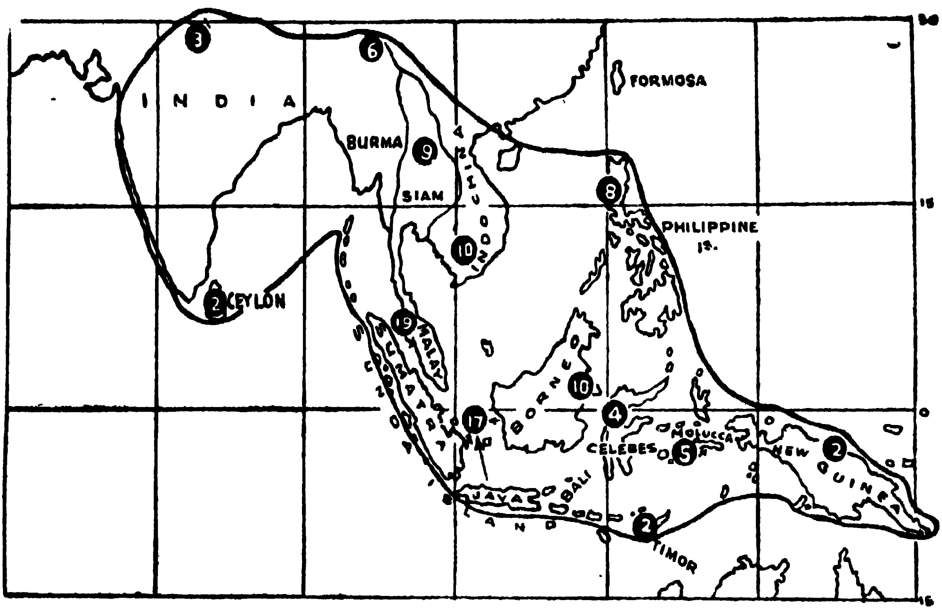
A. glabarata.	*A. tuberosa.*
A. villosa.	*A. guarantica.*
A. marginata.	*A. pusilla.*
A. paragnariensis.	*A. hypogoea.*
A. nambiquara.	*A. rosteiro.*

De Candolle indicates Brazil as the place of origin. Probably it originated from the wild species of Brazil. Waldron divides the species into two sub-species : *fastigata* (bunch) and *procumbens* (spreading) and indicates that *A. prostrata* is progenitor for spreading form and *A. pusilla* for bunch form. The classification into two sub-species is not supported by many others,

JUTE (*Corchorus sp.*). The several species are distributed mostly in the tropical regions of Africa, America, Mexico, India, China, Japan, Madagascar, Formosa, Siam, Java, Malay Peninsula, Philippines and Ceylon. The largest number of species under the genus is in Africa. The jute of commerce is extracted from the two species *C. capsularis* and *C. olitorius*. Cultivation of jute is of recent origin though the plants were known in India long before, mainly as pot herbs and medicinal plants.

MAIZE (*Zea mays*). This is never found in wild state. It has probably originated from teosinte to which it is closely allied. Originated in America. It is hypothesised that selection of teosinte for popping has evolved maize. There are others who believe that its progenitor is extinct. The close relationship between maize and teosinte is assumed to be due to the origin of teosinte as a hybrid between maize and *Tripsacum*. There is yet another hypothesis that maize arose by hybridisation of teosinte with another species now extinct.

MANGO (*Mangifera indica*). Vavilov postulates its origin in the Indian centre. Mukherjee (1951) mentions the introduction of the Mango in the Western hemisphere through the agency of the Spaniards and its introduction into Malaya and other countries of East-Asia by Indian monks in fourth to fifth century B.C. (*vide* Fig. 99-*b*:).



(*From Ind. Jl. Gen. & Pl. Br.*)

Fig. 99-*b*. Map showing natural area of distribution of the genus *Mangifera*. The figures in black circles indicate the number of species in different countries.

MILLETS. (1) Sorghum. (*Sorghum Sp.*). The races of Sorghums are distributed from Africa to India and they were in cultivation from remote times in China and Manchuria. Wild species are abundant in Africa. The 32 races of cultivated Sorghums are distributed with 11 in India and South-Asia and the rest in Africa.

(2) *Eleusine coracana.* De. Candolle considers India as the home of origin while Avdulov considers it to be Abyssinia.

3. *Setaria italica.* -The species *Setaria* are distributed in Africa. India China, Japan and Indian Archipelago are the probable places of origin. *Setaria viridis* is suggested as possible ancestor.

OATS (*Avena sativa*). This has originated in five different centres. (1) Mediterranean for *byzantina* and *sterilis* (2) Abyssinia for *abyssinica*, (3) North-west and Western Europe for *strigosa*, *brevis* and *mudibrevis*, (4) a large area of Asia from Transcaucasia to China for *sativa* and Transcaucasia for *Orientalis*, (5) Chinese centre for *nuda*.

ONIONS (*Allium sp.*). There are eight species under cultivation.

Allium cepa	Onion.
A. sativum	Garlic.
A. porrum	Leek.
A. fistulosum	Japanese onion.
A. ascalonicum	Shallot.
A. schoenoprasum	Ornamentals.
A. neuopolitanum	
A. moly	

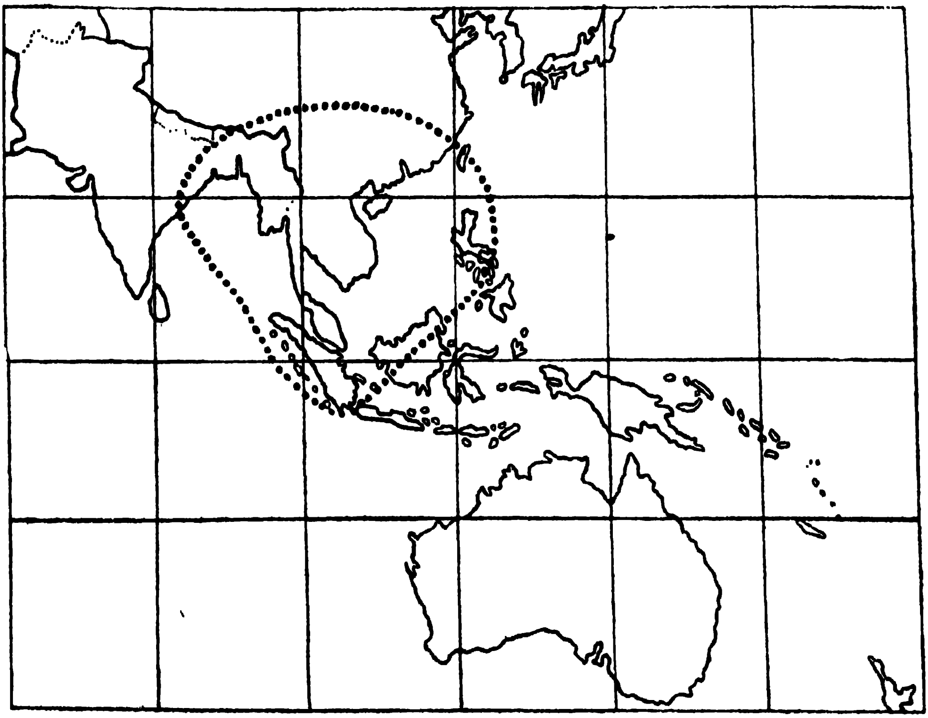
Primary centre is the middle Asiatic region comprising of N.W. India, Afghanistan, Soviet Republic of Tajik, Uzbek and Western Tien states. *A. fistulosum* has its primary centre in China. *A. cepa* has two secondary centres: (1) Near East (2) Mediterranean. *A. sativum* has its secondary centre in the Mediterranean.

POTATO (*Solanum tuberosum*). The cultivated forms arose from the wild species in Chile. There are a large number of cultivated varieties in S. America, whose origins are not clear. The cultivated form is sterile and may be of hybrid origin from prehistoric times in the plateau of Andes. There are 14 species of which the most widely cultivated one is *S. tuberosum*. Of these, 12 species are cultivated in localised areas in Andean countries only.

Salaman (1946) considers that *S. tuberosum* which is widely cultivated in Europe and other places, is a specialised form of *S. andigenum* and is not a separate species. According to him, Potato had its origin in the northern limits of distribution area of *S. andigenum* and that Colombia is the most likely place of origin. From a northern port in S. America it was imported into Spain before 1569 A.D.

RICE (*Oryza sativa*). According to Chatterji (1948) there are 23 species in the genus *Oryza*, 21 wild and two cultivated, *Oryza sativa* and *O. glaberrima*. The centre of origin for the section *sativa* in which majority of the species of *Oryza* are included is Africa. The centre of greatest diversity for the species and the cultivated forms is India.

Future work has to decide the exact centre. to be either India or Indo-China (*Vide* Fig. 99-*c*:) De Candolle



(*From Ind. Jl. Gen. & Pl. Br.*)

Fig. 99-*c*. Centre of origin of Rice.

(1886) thought South India to be the origin of the cultivated rices. *Oryza sativa* var *fatua* occurring widely in South and East-Asia must have contributed to the varietal diversity in India. Ramiah and Ghose (1951) draw attention to the large diversity in the Jeypore tract on the borders of Madras and Orissa States and this may be a secondary centre of origin. That *O. sativa* var *japonica* may be of later development from *indica* is also postulated. Sampath and Narasinga Rao (1951) infer that *O. perennis* is the ancestral form of cultivated rices having given rise to *O. sativa* in Asia and *O. glaberrima* in Africa.

SUGARCANE (*Saccharum officinarum*) —thick cane. It is a native of East Indian tropics. Ritter ascribes its origin to E. Indies, De Candolle to India, Cochin-China or Indonesia. It is of hybrid origin with *S. spontaneum* as one of the parents and the other unknown parent. The place of the process may be Himalayas. On the basis of morphological and geographical evidences, Grassl (1946) suggested that *S. officinarum* is most closely related to *S. robustum* and *Erianthus maximus*. It seems more likely that the main origins were from *S. robustum* by hybridisation with forms of *E. maximus*. The area in which this has taken place appears to be the Fiji islands and New Caledonia.

Parthasarathy (1946) hypothesises that the N. Indian canes (*S. barberi* and *S. sinense*) have arisen as a result of extensive hybridisation between *S. officinarum* and *S. spontaneum* in the regions of Bengal, Bihar and Orissa and naturally this pre-supposes that *S. officinarum* should have been in cultivation in Peninsular India long before the origin of indigenous and N. Indian canes. This hypothesis is supported by the discovery of natural hybrids of *S. officinarum* and *S. spontaneum* in wild state in Orissa by Mukherjee (1949). (Parthasarathy 1951).

TEA (*Camellia Thea*). Assam, China and Manchuria are its home. Cultivated forms are of hybrid origin between the wild broad leaved forms in Burma, N. Siam and Indo-China and the narrow leaved forms of mountain forests of Yunnan and Tonkin.

TOBACCO (*Nicotiana tabacum*). Not found in wild state. It is of hybrid origin and its home is America.

WHEAT (*Triticum sp.*). Vavilov established 166 varietal characters distinguishing various botanical varieties. *Triticum spelta* has originated secondarily. Wheat is regarded as having originated from *Aegilops* by crossing between different species and even with other genera followed by selection and this could have occurred in Mediterranean region or W. Asia. Hard wheat originated in W. Africa.

Chapter 13

STERILITY

STERILITY—ENVIRONMENTAL CAUSES FOR STERILITY—GERMINAL STERILITY—CROSS STERILITY—SELF-STERILITY—GENETIC ASSOCIATION OF STERILITY—CYTOLOGICAL BASIS FOR STERILITY—EVOLUTIONARY SIGNIFICANCE

1. Sterility.—The failure of sexual phase in its various stages of development leading to the non-formation of fruits and seeds is termed '*Sterility*'. This phenomenon is of importance to agriculturists because it reduces yield from grain crops like rice, cholam, etc., though it is of no significance to him in the case of crops like sugarcane, potato, etc., where the propagation is by vegetative parts and the economic products also are from the vegetative parts. In the case of bengal-gram, in one season it was noted that as much as 15% of the plants proved sterile. In the case of G. E. B. 24, an improved strain in rice, the percentage of unset grains varied from 5 to 35 in the different seasonal sowings. Loss of grain yield due to sterility may vary from 0 to 100 per cent depending upon the factors causing the same. The extent of sterility in respect of some plants is shown below :

TABLE 51.

Name.	% sterility.
Achras sapota (Sapota)	20
Adhatoda vasica (Adhatoda)	10—20
Andropogon pertusus	10—15
Aristolochia bracteata	5—6
Cassia siamea	80
Citrus aurantium (Orange)	3
Cocos nucifera (Cocoanut)	90
Convolvulus arvensis (Field bind Weed) ...	75
Crotalaria juncea (Sunnhemp)	5
Cynodon dactylon (Hariali grass)	3—5
Cyperus bulbosus (Bulb grass)	15
C. rotundus (Nut grass)	80
Dolichos Lablab (Field bean) .. .	5
Hibiscus rosa sinensis (Shoe flower)	98
Millingtonia hortensis (Indian Cork tree) ..	70—80
Panicum maximum (Gunea grass)	50
Rosa damascana (Rose)	25
Saccharum officinarum (Sugarcane)	50
Thespesia populnea (Portia tree)	90

Sterility is an important problem in breeding trials. A plant breeder attempts to cross individuals which differ in respect of morphological or physiological characteristics and select useful recombinations from the progenies of the cross. Sterility of the hybrid is a hindrance to his attempts.

Since sterility concerns the sexual mechanism in plants, it is intimately connected with the normal production and functioning of flowers in the same. *Sterility may be brought about by (i) malformation of essential sexual organs* (*Fig.* 100) (ii) *by degeneration of cell mechanism in the formation of gametes* (iii) *degeneration of zygote.* The derangement in the normal functioning of sex may be caused by part or whole set of chromosomes or by one or more genes. The cytological details are discussed later.

(*Photo from Cotton Specialist.*)

Fig. 100. Sterility in bengal gram due to fasciation in essential organs of the flower.

There seems to be no relationship between the vigour of somatic development and sterility. While the plant may grow vigorously or sometimes better than the normal, the sexual organs may fail to develop or function normally and show sterility to varying degrees.

Sterility may be classified as follows :

- Sterility.
  - Environmental.
    - nutrition.
    - light.
    - humidity.
    - diseases.
  - Germinal.
    - Incompatibility.
      - Evolutionary.
      - Genetic.
        - cross sterility.
        - self-sterility.
    - Impotence.

2. **Environmental causes for sterility.**—It has been pointed out that environment has large influence on the flowering and fruiting in a plant. Environmental factors such as nutrients in soils, atmospheric conditions and pests and diseases bring about changes in the normal nutrition of the plant and thereby affect formation and setting of fruit. Sterility brought about by environment is discussed in this section.

In rice there are a few varieties that show sterile tip (Fig. 101). The sterile spikelets are formed due to under-development of both pollen and ovule. When such varieties are raised in rich soils or fields heavily manured with nitrogenous manures, the extent of sterile tip increases. In general, nitrogenous manures encourage vegetative growth and increase sterility.

(Photo from Paddy Specialist.)

Fig. 101. Sterile tip in rice.

At Coimbatore, seasonal sowings in respect of two varieties of rice were conducted in 1927–28. The percentage of sterility in respect of different sowings is shown in table 52.

Time of flowering and yield in respect of many crops depend upon the time of sowing as shown above. The percentage of sterility will vary with varieties as indicated by the data in table 52.

From the yield per plot and the average number of spikelets per plant it is seen that the vigour of somatic development has no influence on the percentage of sterility.

Flowering in sugarcane is seasonal and seldom occurs outside the tropics. Some varieties flower regularly while others flower only when seasonal conditions are favourable, *e.g.*, Fiji B flowers profusely on West Coast while at

TABLE 52.

Time of sowing.	G.E.B. 24. Total yield of plot in gms.	G.E.B. 24. Average No. of ears per plant.	G.E.B. 24. % of unsetting.	*Co* 3. Total yield of plot in gms.	*Co* 3. Average. No. of ears per plant.	*Co* 3. % of unsetting.
July ..	4820	7·1	19·2	5720	5·1	15·7
August ...	4750	6·8	23·3	5360	5·9	13·1
September	3890	6·4	27·1	4260	5·1	30·7
October ...	4140	7·4	15·1	3810	5·4	19·1
November	3050	7·4	18·6	2690	5·5	9·9
December	2740	6·6	15·3	4820	6·2	13·9
January	820	8·3	35·3	570	7·8	31·8
February	4880	8·8	5·8	2390	6·6	12·6

Coimbatore it flowers only when seasonal conditions are favourable. Some varieties are male sterile, *e.g.*, Vellai and P.O.J. 2725 of Coimbatore. A variety may be male sterile in one locality and female sterile in another or it may change its behaviour after some time. ' Saretha ' was male sterile first at Coimbatore but later it produced profuse pollen. *S. spontaneum* from Lahore did not flower under Coimbatore conditions. CO. 421 which is a pollen sterile variety developed healthy pollen with 10% germination when the plants are subjected to 15 hours light period (Yusuf 1946). The arrowing and fertility of sugarcane varieties in different regions provide a good example of sterility in relation to environment. Kraus and Kraybill showed in tomato that fruiting depends upon a suitable relationship between mineral salts and starches and sugars manufactured by the plant. They report four conditions. (1) Weakened vegetation and non-fruitfulness resulting from abundance of moisture and mineral nutrients without an available carbo-hydrate. (2) barrenness and sterility increase due to abundance of moisture and mineral especially nitrates coupled with carbo-hydrate supply, (3) fertility lessens vegetation and fruitfulness results from decrease in nitrates in proportion to carbo-hydrate. (4) Suppression of both vegetation and fruitfulness results from a further reduction of nitrate without inhibiting a possible increase of carbo-hydrates.

The relative percentage increase in vegetation and seed production in some leguminous crops caused by an addition of nitrogen to soil is shown in table 53.

TABLE 53.

Treatment.	Indigo.			Gram.			Sweet peas.		
	Dry weight in grams.			Dry weight in grams.			Dry weight in grams.		
	Vegetation.	Seed.	Veg./Seed.	Vegetation.	Seed.	Veg./Seed.	Vegetation.	Seed.	Veg./Seed.
Control	68	32	2·19	719	409	1·76	994	259	3·84
Organic matter well rotted leaf mould 10% by vol.	...	...	...	1158	403	2·87	2175	535	3·99
Organic matter well rotted leaf mould 30% by vol.	907	577	1·56	1136	361	3·14	2201	526	4·19
Organic matter well rotted leaf mould 50% by vol.	...	. .	...	1276	421	3·03	2351	525	4·48
Sodium nitrate ...	...	...	...	...	...	...	...	...	...
2 cwt. per acre	...	...	...	1170	627	1·87	1190	398	2·99
4 cwt. per acre	...	...	...	1127	651	1·76	1255	356	3·41
8 cwt. per acre	191	115	1·66	...	...	...	...	...	...

The table shows that the same manurial treatment has different effect on the crops like indigo, gram and sweet peas.

Weather conditions have great influence in setting and development of fruits. In the case of cotton, humidity and temperature at the time of flowering determine the percentage of setting in flowers. Late season flowers are easily shed. Premature abscission of flowers in many cases leads to sterility of the plants. The effect of cloudy days on flower opening and fruit setting in bengal-gram is shown in table 54.

TABLE 54.

Variety.	% Setting in flowers opened during cloudy weather.	Setting in flowers opened after cloudy weather.
*T*1	7·5	48·5
*T*2	11·1	67·5
*T*18	17·8	84·0
*T*25	5·2	73·0

In flowers that open on cloudy days setting is poor while in the case of flowers that open after cloudy weather, setting is high. This effect might be due to premature bursting of anther sacs or the adverse effect of weather on the pollinated pollen and stigma.

In rice blooming is conditioned by atmospheric temperature. If the temperature and humidity are artificially raised, the flower opens, stamens elongate and the anthers are protruded but stigma remains inside the lemma and palet, and when the latter close, the stigma is prevented from emerging and getting pollinated. When the above mentioned condition takes place in nature, the spikelets fail to set seed for want of pollination.

It is known to students of Agriculture that pests and diseases cause sterility either by preventing normal development of flowers or by cutting off nutrition to the flowers and fruits. Stem borers, for example, bore into the stem and this prevents the normal supply of nutrients to the growing portions. In the case of rice crop, it is common to see sterile white ears when the crop is attacked by stem borer. The damage by rice bug is another example where sterile spikelets are formed due to the sucking of the plant sap by the bug. Similarly many other fungus diseases bring about sterility. Irritation by insect damage or parasitic fungi may induce fasciation in the floral parts. In the case of little leaf disease of cotton, the floral parts undergo fasciation. In the green ear disease of cumbu, the floral parts develop into leaf like structures.

3. **Germinal sterility.**—Sterility may be due to defects in the germinal material. The pollen and the ovule may either be malformed or they may

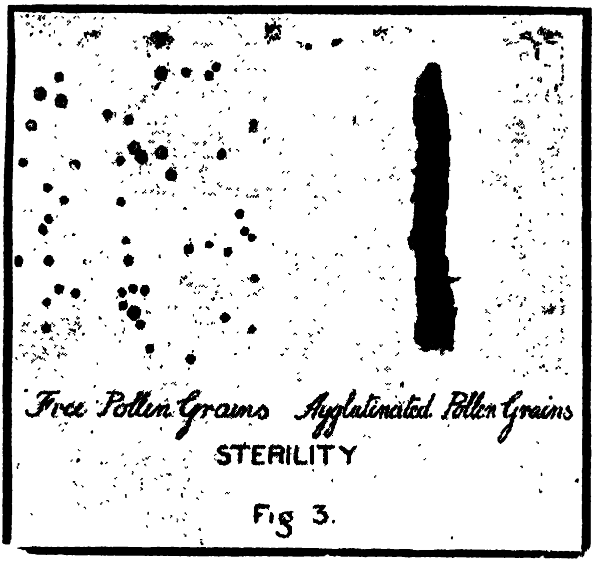


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Fig. 102. Agglutinated pollen grains in ragi (*Eleusine coracana*).

not function under certain conditions due to genetic causes. In *Gossypium herbaceum* a case of female sterility was noted. Pollen was normal but the

pistil was malformed. The style was small and triangular and was not receptive. This malformation was heritable and the gene recessive to normal (Stg.-stg). Non-functional or aborted pollen grains may be formed to varying degrees. In cholam empty anther sacs without pollen were noted. In ragi, agglutinated pollen grains were formed (Fig. 102). The plant proved to be sterile while the stigma was fertile. Earheads did not set seed. This male sterility proved to be simple recessive to normal (Ms-ms). Sterility may also be caused by the premature shedding of flowers and the shedding may be a genetic factor as in the case of wild sorghums. The above stated conditions lead to impotency of the gametes concerned. There are other instances where the gametes may be well formed without any morphological defects but yet they may function in certain combinations only. The plants may prove self incompatible or cross incompatible resulting in self-sterility or cross sterility respectively.

4. Cross sterility.—Inter specific crosses generally fail or hybrid may prove sterile. Sterility in species crosses may result from any one of the following causes.

(1) *Physiological.*—The pollen tube does not germinate and grow normally in the stigma of the other species.

(2) *Chromosomal.*—There being no balance between the two chromosome complements, the zygote fails to further differentiate.

(3) *Meiotic.*—The zygote may develop normally but yet the mature plant is sterile due to meiotic irregularities.

Physiological.—The pollen grain may be prevented from the germination by the secretions on foreign style or stigma. In plums, there is a definite layer in the style which inhibits the further growth of the pollen tube. Though the stigma is receptive and the pollen grains germinate, the pollen tube does not go beyond lower half of the style. In the case of apples and tobacco, the non-fertilisation resulted due to the very slow growth of the pollen tube in the foreign style. In the case of *Datura*, the slow pollen growth showed a correlation to the chromosome numbers in the pollen and stigma. 4n pollen grows satisfactorily on 4n styles while 2n pollen grows well on n, 2n, 3n and 4n styles. In the case of interspecific cross *Gossypium herbaceum* × *G. hirsutum* in cotton, successful results were achieved by treating the stigma prior to pollination with dilute solution of cane sugar and citric acid. Another interesting example is that of *Polemonium mexicanum* whose pollen tube is not long enough to reach the ovule in *P. pauciflorum*.

Chromosomal.—When the two chromosomal complements differ very much, fertilisation will fail even though the pollen tube may reach the egg. In *Nicotiana rustica*, on selfing, fertilisation and development are normal but on out-crossing with distant forms like *N. glutinosa*, *Petunia violacea* and *Lycopersicum esculentum*, the crosses fail. In all the crosses, double fertilisation occurs and the fertilised embryo and endosperm start growth but the development of endosperm is not normal from the beginning. Nucellus which is one layered in normal plants becomes meristematic in the hybrid and multi-layered.

It overgrows endosperm at chalazal end and occludes it. Vascular bundles in the developing region are normally developed. Hyperplasia of nucellus or inner integument is the developmental feature and this type of sterility is termed " *somato plastic sterility* ".

When fertilisation has been successfully effected, sterility may result from the disproportionate development of different parts of the seed. In the case of the cross *Linum perenne* × *L. austriacum*, the embryo is shrivelled and consequently the cross proved sterile. When the shrivelled embryo was removed from the testas at the proper stage of its development and raised in artificial culture media, viable plants could be raised. The disproportionate size of embryo in relation to that of seed is the cause of sterility in this cross.

In the case of a cross between *Datura stramonium* and *D. metel*, fertilisation was effected but the endosperm began to develop before the embryo. The division of endosperm cells upto 7th day is normal after which they begin to disintegrate. Pro-embryo development upto 5 to 7 days is normal but later it also disintegrates.

In the case of crosses between two distant forms, not only the chromosome numbers and fertilisation that matter but also there must be genetic balance between the two chromosome sets for the normal development of the hybrid. Lack of such genetic balance between the chromosomes of the two parents brings about sterility.

In the case of tobacco, a large number of interspecific crosses have been made. *Nicotiana glauca* (n–12) × *N. plumbaginifolia* (n–10) was more successful than the reciprocal cross. In all other cases too, where the parental species differed in chromosome numbers, crosses succeed only when the species with larger number is used as female parent.

In the case of normal diploids, the chromosome numbers in style, fertilised egg and endosperm are in the proportion 2n : 2n : 3n. If this proportion is very much disturbed, the fertilisation and subsequent development of the zygote is also disturbed. Taking the reciprocal cross between a diploid and an autotetraploid, the abovementioned proportion is upset as shown in table 55.

The proportion of chromosome complements in different tissues in cross (*b*) is nearer to that in (*c*) than that of (*a*). This enables the various parts of the seed to develop normally while in (*a*) this is not possible.

TABLE 55.

Cross.	Style.	Fertilised egg.	Endosperm (after fertilisation).
(*a*) Diploid × Tetraploid ...	$2n$	$3n$	$4n$
(*b*) Tetraploid × Diploid ...	$4n$	$3n$	$5n$
(*c*) Diploid × Diploid ...	$2n$	$2n$	$3n$

Meiotic.—Two species may cross but the hybrid plant may prove sterile. This is termed *hybrid sterility*. The development changes in the somatic tissues do not affect the processes in the formation of gametes. The development of plant body is not related to its reproductive phases. Sometimes the sterile hybrid may be more vigorous than the parents. In D. *pseudo-obscura*, the male hybrid from the cross between A and B races is sterile due to irregular spermatogenesis. Testes of the hybrid were transplanted into normal parent larva and yet the spermatogenesis of the transplanted testes was abnormal. This proves the independence of the sexual mechanism to somatic tissues.

In any case, the chromosome behaviour in the hybrid has been the main cause for sterility. The chromosomes of the parental species fail to pair and form bivalents at meiosis. Meiotic irregularities such as scattering of chromosomes throughout the spindle at metaphase I, irregular and unequal anaphase separation, extrusion of chromosomes into cytoplasm, lagging chromosomes, chromatin bridge formation etc., lead to sterility. Partial or complete sterility results due to structural differences in chromosomes of the parents and these have been already discussed in an earlier chapter.

In the case of the cross *Gossypium anomalum* × *G. arboreum*, the F_1 was partially sterile and the chromosome pairing is indicated in table 56.

TABLE 56.

	Univalents.	Bivalents.	Trivalents.
G. anomalum ($n = 13$) × *G. arboreum* ($n = 13$) ...	3·70	10·70	0·10

The chromosome pairing is variable and the number of univalents varied from 0 to 14, and the formation of 13 bivalents is due to allosyndetic pairing. Since the formation of functional gametes and their mating is rare, the hybrid set few bolls.

In table 57, the chromosome association in metaphase I of the hybrid *Nicotiana glauca* (n–12) × *N. plumbaginifolia* (n–10) is shown.

TABLE 57.

No. of bivalents.	% of cells.
3	3
2	15
1	25
0	57

The hybrid showed the following abnormalities at meiosis : Unequal bivalents at diakinesis and metaphase I, formation of chromatin bridges at anaphase I and II, formation of restitution nuclei at the end of division I.

Hybrids between polyploids show variable pairing depending upon the degree of relationship between them. Autosyndesis or allosyndesis may be evidenced. Autosyndesis indicates that each parent carries more than one genom bearing partial homology. Allosyndesis indicates the homology between the genoms from the two species entering the cross. In the cross *Papaver nudicaule* (*n*—7) × *P. striatocarpum* (*n*—35), a fertile hybrid with 21 bivalents are formed by auto-syndetic pairing in *P. striatocarpum* and allo-syndetic pairing between 7 chromosomes from the two species.

There are a few instances where the chromosome pairing and disjunction are apparently normal but yet the hybrid is sterile : *e.g.*, *Digitalis lanata* × *D. micranta*, *D. purpurea* × *D. ambigua*, *Lolium perenne* × *Festuca pratensis*.

The reduction division in species hybrids is classified as follows by Federly (1927) based on chromosome conjugation :

(1) *Drosera type* in which homologous chromosomes conjugate, the rest remaining as univalents.

(2) *Pygaera type* in which conjugation of chromosome rarely if ever occurs.

(3) *Boreale type* in which only some of the chromosomes conjugate in spite of the presence of partners for the others.

More than one sterility mechanism may exist in a hybrid, chief of which is probably the failure of chromosome pairing. Depending upon the stage when the sterility mechanism sets in, it is classified as (1) *gametic where non-functional gametes are formed* (2) *zygotic where inviable zygotes are formed.* Muntzing (1930) uses the terms 'haplontic' and 'diplontic' sterility.

5. **Self-sterility.**—Some species are self sterile, i.e., seeds do not set when the plants are selfed. The floral parts are all well developed and the stigma and pollen appear normal. The sterility here is not due to difference in the period of pollen shedding and stigma receptivity as was pointed out in the case of *cumbu* but even when functional pollen grains are dusted on to the stigma, seeds do not set. It must be remembered that the pollen tube and embryo sac represent the haploid generation and these are short lived and are entirely parasitic on the diploid sporophyte. In higher plants, the pollen that falls on the stigma is separated from the ovule by the intervening maternal tissues. The pollen is enclosed in anther sac and the ovule in the carpellary chamber. The pollen after being shed, falls on the stigma and grows down the style and reaches the egg cell enclosed in the ovule. The separation of the two gametes by diploid tissue is an important factor in successful fertilisation. The pollen tube has to penetrate the stigma and style before the male gamete can meet the female gamete. *Any adverse interaction between the pollen tube and the stigmatic or stylar tissues may lead to sterility, and this interaction may be physiological or genetic.* The separation of the two gametes by diploid tissues is by itself a contrivance for encouraging cross pollination but in many

cases, this contrivance by itself is not effective. Therefore the plants have developed further physiological and genetic contrivances by which either the pollen tube is effectively prevented from reaching the egg or the fertilisation fails or the zygote does not develop normally. The physiological causes for sterility described under section 4 of this chapter may form the basis for self-sterility also. The following are a few instances where self-sterility has been studied.

Notylia ...	Muller (1868).
Linum grandiflorum ...	Darwin (1877).
Brassica pekinensis	Stout (1931).
Cherries (diploid)	Alify (1933).
Some varieties of apples ..	Hall and Crane (1933).
Capsella grandiflora ..	Riley (1938).
Melilotus officinalis ..	Brink (1934).
Cardamine pratensis ...	Correns (1912).
Brassica oleracea Var. italica. ..	*Sears* (1937).
Raphanus sativus	*Sears* (1937).
Secale cereale	*Sears* (1937).
Potatoes	Pal (1941).

In most of these cases, the incompatible pollen either completely fails to germinate or the tube fails to grow beyond the stigmatic branches. The stigma seems to secrete some substance which inhibits pollen tube growth. It is believed by some that the failure of the stigma to secrete stimulating substances is the cause, but it is not likely to be so due to the fact that the pollen grains germinate normally in sugar solutions. In such of the cases where the stigma secretes inhibiting substances, self-sterility can be overcome by scraping the outer tissues of the stigma. The seed setting in Broccoli where the stigma was removed and the flower selfed is an example of this type.

Broccoli : yields of seed from mutilated flowers, self-pollinated and kept in moist chamber are shown in the following table :

TABLE 58.

Treatment.	Number of seeds.
Portion of pistil removed	.....
Stigma half-style removed	12, 16, 15
Stigma one-fourth style removed	7, 10
Stigma removed	17, 13
One-half stigma removed	15, 24
Thin layer of stigma removed	22, 19
Stigmatic surface macerated	20, 18
Stigma much cut	0, 1

In some instances, the self-sterile plants show " bud fertility ", *i.e.*, if the flowers are self-pollinated before the flower normally opens, setting is good. Bud fertility has been noted in the following cases:—

Nicotiana sp. ...	East (1923).
Verbascum phœniceum ...	Sirks (1926).
Petunia violacea	Yasuda (1930).
Brassica pekinensis ...	Kakizaki and Kasai (1933).
Raphanus sativus	Kakizaki and Kasai (1933).
Eruca sativa	Alam (1938).
Brassica ole Racea Var capitata.	Pearson (1929).
Broccoli ..	Sears (1937).

Yields of Broccoli seed from bud pollinated incompatible flowers are shown in table 59.

TABLE 59.

Plant No.	Days pollinated before opening.											
	0	1	2	3	4	5	6	7	8	9	10	11
1 ...	0, 0	0, 0, 0	...	10, 18	...	...	...	18. 13	...	...	...	...
2 ...	0, 0, 1, 3	2, 0	2, 9, 0	10, 14	16, 20	14. 20	18, 18	16	...	...	...	..
3 ...	1, 1	8, 2	21	11, 9	16	...	22	17	13	...	...	4

(*Data from Sears.*)

The data show that the flowers are fertile from 7 days prior to flower-opening.

Self-sterility in other cases may arise due to the slow growth of the pollen tube in the stigmatic tissues and the flowers may get abscissed before fertilisation can take place. This slow rate of growth may either be conditioned by environment or genetic factors. In the case of Columbian potato, *Solanum rybinii*, it was possible to effect fertilisation and normal developments by altering external conditions.

Self-sterility may be evidenced even after fertilisation has been effected. In these cases, fertilisation proceeds normally, but degeneration of the zygote sets in due to various reasons. Such an instance was noticed by Sears in *Gasteria verrucosa*. The incompatibly fertilised ovules began to degenerate in 48 to 96 hours after fertilisation and also the division of endosperm nucleus did not progress and the integument of the ovules also showed early signs of degeneration.

Self-sterility of the *gasteria type*, viz., the degeneration after fertilisation is rare in higher plants. In generality of cases, the pollen either completely fails to germinate, or the tube growth is not sufficient enough to reach the ovule. The inhibition of normal tube growth is explained differently on the basis of genetic constitution of the pollen and stigmatic or stylar tissues. Genetic analysis of self-sterility has been extensively carried out in *Nicotiana* and *Brassica* species. Kunth (1906) gives a list of 134 self-sterile species from both monocots and dicots.

There are two hypotheses to explain self-sterility in higher plants (i) *oppositional factor* hypothesis of East and Mangelsdorf (1925) (Fig. 103) and (ii) *Lythrum salicaria* scheme of VonUbisch (1921). The former type of self-sterility is of widespread occurrence in higher plants and has been worked out in a number of cases. The following is an example from potato where self-sterility has been explained on the basis of oppositional factor hypothesis.

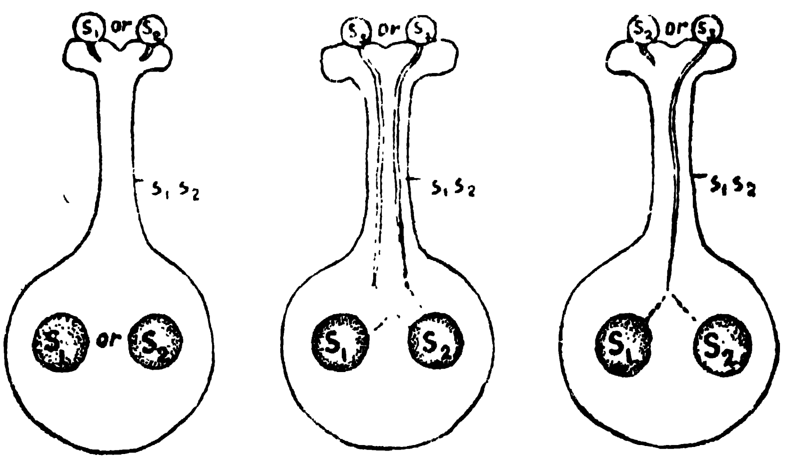

Fig. 103. To illustrate self-sterility on the oppositional factor hypothesis.

Note- That the pollen grain, carrying a factor that is also present in the maternal tissues, fails to germinate and function normally.

It is assumed that there are a series of allelomorphs designated S^1 S^2 S^3 ....S^n. Pollen tube growth is inhibited when the same S factor is present both in the pollen tube and the stigmatic tissue. For example, if the pollen is of S^1 and the stigma is of S^1 S^2 constitution, the plant proves sterile. The factor S^1 is present both in the pollen and stylar tissue and hence the pollen tube growth is inhibited. The stigma and pollen must bear different alleles and then only they prove compatible.

At the Simla potato breeding station, experiments on 16 varieties of *Solanum caldasii* and one variety of *S. subtilis* were conducted. The former gave five intra sterile but interfertile groups and *S. subtilis* formed the sixth group. Four crosses between these representative six groups gave 18 groups A – R which on further intercrossing tests, fell into 8 genotypes for self-sterility as presented in table 60.

TABLE 60.

			$S_1 S_2$				$S_1 S_3$	$S_1 S_4$			$S_1 S_5$		$S_2 S_3$	$S_2 S_4$			$S_2 S_5$		$S_4 S_5$	
			A	F	H	O	C	D	G	P	L	Q	B	E	K	R	J	M	I	N
$S_1 S_2$	A	...	—	—	—	—	×	×	×	×	×	×	×	×	×		×	×	×	×
	F	...	—	—	—	—	×	×	×	×	×	×	×		×	×		×	×	×
	H	...	—	—	—	—	×	×	×	×	×	×	×	×	×		×	×	×	×
	O	...	—	—	—	—	×	×	×	×	×	×	×	×		×	×	×	×	×
$S_1 S_3$	C	...	×	×	×	×	—	×	×	×	×	×	×		×				×	×
$S_1 S_4$	D	...	×	×	×	×	×	—	—	—	×	×	×	×	×	×		×	×	×
	G	...	×	×	×	×		—	—	—	×	×	×	×	×	×	×	×	×	×
	P	...	×	×	×	×	×	—	—	—	×	×	×	×			×	×	×	×
$S_1 S_5$	L	...	×	×	×	×	×	×		×	—	—	×	×	×	×	×	×	×	×
	Q	...	×	×	×	×	×	×	×	×	—	—	×	×	×	×	×	×	×	×
$S_2 S_3$	B	...	×	×	×		×	×	×		×	×	—	×	×	×	×	×	×	×
$S_2 S_4$	E	...	×	×	×	×	×	×	×	×	×	×	×	—	—	—	×	×	×	×
	K	...	×	—	×	—	×	—	×	—		×	—	—	—	—	×	...	×	—
	R	...	×	×	×	×	×	×	×	×	×	×	×	—	—	—	×	×	×	×
$S_2 S_5$	J	...	×	×	×	×	×	×	×		×		×	×	×	×	—	—	×	×
	M	...	×	×	×	×	×	×	×	×	×	×	×	×	×	×	—	—	×	×
$S_4 S_5$	I	...	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	—	—
	N	...	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	—	—

— Cross and self-incompatible combinations. × Cross compatible combinations.

As has been already pointed out, self-sterility due to S. factors is the most common type. The *Lythrum salicaria* scheme is applied only to (1) *Lythrum salicaria, Oxalis voldiviana,* and to *Capsella grandiflora.* This theory involves two pairs of factors Aa, Mm of which A is epistatic to M. The pollen reacts in accordance with the diploid constitution of the plant from which it came.

6. Genetic association of sterility.—Sterility may be associated with other economic characters. In other words, the genes causing sterility may be situated on any of the chromosomes and thereby be linked with other useful genes. In the case of panicle tip sterility in *Sorghum* the primary and secondary branch lengths were 14·5 c.m. and 4·0 c.m. against 17·5 c.m. and 6·5 c.m. in normal cases. There was reduction in the number of sessile spikelets, the average number in sterile heads being 800 only as against double that number in normal earheads.

In a family of a cross in rice, segregating for anthocyanin pigment in leaf sheath and axil, the sterility was found associated with the pigment as shown in table 61.

TABLE 61.

% OF SETTING IN PIGMENTED AND NON-PIGMENTED PLANTS.

Percentage of set spikelets.	Pigmented.	Non-Pigmented.
0—4	1	...
5—9	2	1
10—14	1	1
15—19	3	...
20—24	4	...
25—29	6	3
30—34	17	2
35—39	30	2
40—44	45	1
45—49	64	4
50—54	109	16
55—59	76	17
60—64	44	24
65—69	20	45
70—74	13	60
75—79	19	104
80—84	14	118
85—89	11	124
90—94	4	57
95—99	3	26
Mean.	53·7 ± 0·43	78·2 ± 0·34

Sterility is more in the pigmented group. In another instance where the pigment was in the glumes, the pigmented type proved more fertile than the green glumed progenies. Poor emergence of panicle was associated with sterility. (Fig. 104).

In the same crop, grain size and arrangement on panicle were associated with sterility. Small grain with closely packed arrangement in panicle showed

more of sterility than those with big grain and sparser arrangement. Glutinous endosperm and presence of awn are also closely associated with sterility.

(*Photo from Paddy Specialist.*)

Fig. 104. Panicles from F_2 to illustrate the association between sterility and emergence of panicle in rice.

In maize, pollen sterility and resistance to smut were linked.

Self-sterility in more than 800 species has been investigated. It is evident in groups of plants which are predominantly herbaceous. Self-sterility is of recent origin in the evolution of plants. Herbaceous plants had their origin from primitive woody types and therefore self-sterility is most prevalent in these. It is a mechanism to promote variation and perpetuate heterozygosity and hence plays vital role in evolution.

7. Cytological basis for sterility.—It has been pointed out that a single Mendelian factor may cause sterility, *e.g.*, a factor for asynapsis. Sterility

in such cases may be due to defective development of pollen or egg or if lethal factors are involved the fertilised egg may be aborted. That sterility is of recent origin has been mentioned. It is largely to be expected in the progenies of interspecific and intergeneric crosses where meiotic irregularities lead to the failure of the formation of gametes. Polyploids of recent origin exhibit sterility due to multivalent association of chromosomes in meiosis. A case of auto-tetraploid was discussed in chapter X. Aneuploids and auto-triploids also show sterility to varying degrees. In the auto-tetraploids as well as in some amphidiploids by selfing and selection in the first few generations after their origin meiotic irregularities are eliminated and self-fertility is restored. This has been pointed out to be so in the case of bengal gram and *B. juncea*.

In all the above mentioned cases, failure, complete or partial, to form normal gametes results from irregularities in the first or second of meiotic divisions. Formation of multivalents as in auto-tetraploids or the presence of univalents as in triploids and aneuploids leads to irregular separation of chromosomes at anaphase I. The two nuclei resulting from division I, bear unequal number of chromosomes. With increase in the chromosome number over the haploid set, the gametes become increasingly non-viable. When fertilised by a normal haploid gamete, the forms with increased number of odd chromosomes result, *e.g.*, (2n + 1), (2n + 2), (2n + 3), etc. With increase in the number of unbalanced chromosomes, the plants are more stunted and sterile than the forms with less number of odd chromosomes. In rice, the triploid gave rise to aneuploids with 25 to 29 chromosomes.

The irregularity in chromosome conjugation increases with the odd chromosomes ; in some cases elimination of zygote and germinating seeds may also occur. The variable chromosome conjugation in rice with 2n-27 is shown in table 62.

TABLE 62.

CHROMOSOME ASSOCIATION.

$9_{II}-3_{III}$	$10_{II}-2_{III}-1_{I}$	$11_{II}-1_{III}-2_{I}$	$12_{II}-3_{I}$	$13_{II}-1_{I}$	$10_{II}-1_{III}-4_{I}$	$10_{II}-1_{IV}-3_{I}$	$9_{II}-1_{IV}-5_{I}$
4	4	2	6	1	2	1	1

In the case of a sterile 'til' (*Sesamum orientale*), P.M.C. instead of forming tetrads, showed varying numbers of daughter nuclei as shown in table 63.

TABLE 63.

Number of cells per P.M.C.	Frequency.
2	17
3	9
4	30
5	7
6	44
7	2
8	6

P.M.C. with 6 daughter cells are the most frequent ones. By crossing tests, the non-functional nature of all the pollen grains was confirmed.

The chromosomal aberrations in a sterile *Sesamum* during meiosis in P.M.C. are summarised in table 64. (Fig. 105).

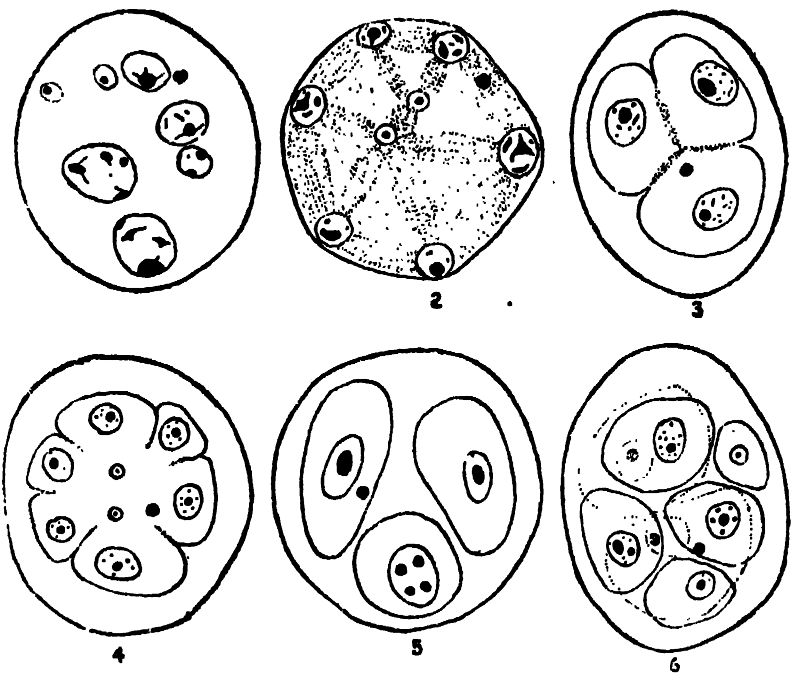

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Fig. 105. Meiosis in a sterile gingelly plant. 1. A cell with 7 nuclei of unequal size. 2. A cell with 8 nuclei. 3. Three daughter cells with secondary nucleolus enclosed in one of them. 4. Furrowings of cytoplasm. 5. One of the cells showing four nucleoli in the nucleus. 6. Seven daughter cells.

The irregularities mentioned in table 64 may be taken as common in sterility due to chromosomal aberrations.

Beadle and McClintock (1928) and Beadle (1930, 1932, 1933) in maize, Satina and Blakeslee (1935) and Berger (1935) in *Datura*, Gregory (1905) and Faberge (1937) in *Lathyrus odoratus*, Koller (1938) and Sansome in *Pisum sativum* describe abnormal meiotic phenomena which are determined by genes which lead to unusual numbers of chromosomes in the gametes. These genes interfere with chiasma formation or with normal disjunction by causing the chromosomes to be '*sticky*'.

Structural changes in chromosomes arising out of irradiation may also cause sterility. A case of semi sterility in rice obtained by irradiating the seed has been described in an earlier chapter.

8. Evolutionary significance.—Sterility is essentially a mechanism connected with sexual reproduction in plants. In the course of evolution of plants,

TABLE 64.

I Division spindle.	Mode of chromosome separation.	Number of nuclei at telophase I.	II Division.	Number of nuclei at telophase II.	Number of daughter cells.
Bipolar with bivalents and univalents.	Separates into two unequal groups.	Two unequal sized nuclei.	Regular equational division.	4 nuclei . 2 unequal pairs.	4
			Fusion of spindles	2 equal sized (2*n* nuclei).	2
			Failure of II Division.	2 unequal nuclei ...	2
			Regular equational division.	3 pairs of unequal nuclei.	6
			2 nuclei divide and one does not.	Five nuclei ...	5
Bi or tri polar spindle.	Into three unequal groups.	3 unequal nuclei ...	1 nucleus divides and 2 do not.	Four nuclei ...	4
			Any of the above with lagging of chromosomes.	Upto 8 ...	Upto 8
			Failure of II Division.	Three ...	3
			Regular equational division.	8 nuclei 4 pairs ...	8
Do. ...	Into four unequal groups.	4 unequal nuclei ...	Failure of one or more nuclei to divide.	Less than 8 ...	Less than 8
			As above and lagging of chromosomes.	Upto 8 ...	Upto 8
			Failure of II Division.	Four ...	4
Do. ...	Into two to four and lagging chromosomes.	Two or four ...	With one or the other of the above types.	Upto 8 ...	Upto 8

the sporophyte developed contrivances to separate the male and female gametes by developing sterile tissues surrounding them. It also developed floral contrivances that encouraged cross-pollination. The latter is important in evolution, because new characters and variations are introduced into a population by hybridisation. *A continuous series of variations can be established by out-crossing and to encourage it to the maximum, self-sterility is developed.*

While self-sterility helps to increase variation by out-crossing, it is essential to break the continuity of variation to establish distinct species.

In chapter XII it was pointed out that isolation—genetic or geographic—is an important requirement in the evolution of new species. *Where no geographic barriers exist between any two groups of plants, cross-sterility serves the same purpose.* The two groups do not cross, or if they cross the hybrid is sterile and therefore there can be no recombinations in further generations. This results in the evolution of the two groups into distinct types without intergrades between them. The changes may be in the gene constellations of the two species or in the structure of the chromosomal complements. These differences accumulate in course of time and hybridity at a later stage results in sterility. In Nature, provisions are made to overcome this sterility by doubling the chromosome compliments in the hybrid. This may result in the evolution of new species as in the case of *Primula kewensis* or *Brassica juncea.* Aneuploids may form the basis for secondary polyploidy and a new series of species as is indicated by the probable origin of *Oryza sativa.*

Chapter 14

QUANTITATIVE CHARACTERS

QUANTITATIVE VARIATIONS - TYPES OF F_1 AND F_2 -EFFECT AND LOCATION OF MULTIPLE FACTORS--QUANTITATIVE MEASUREMENTS.

1. Quantitative variations.—The seven pairs of characters studied by Mendel were such that they could be qualitatively described, *e.g.*, smooth *vs.* wrinkled, green *vs.* yellow and so on. When the character pairs segregated in F_2, the parental types reappeared and there were no intergrades. The segregation was sharp and in such cases, the classification of the phenotype of the F_2 population was easy. *Such qualitative characters are generally* governed by one or two pairs of genes.

Obviously, all characters do not lend themselves for accurate qualitative description. For example, yield of crops, size of grains, duration in days, chemical composition of the produce, etc., have to be measured quantitatively in the appropriate units of measurement. In such characters, when a large number of individuals of a population are measured, the recorded values do not fall into definite groups, but the variation is continuous. If 200 grains of paddy are measured, all the recorded values may not be 4·8 m.m. but the readings may vary from 4·6 to 5·0 m.m. with the average as 4·8 m.m. It is therefore not possible to describe a quantitative character by a single measurement but the phenotypic value is judged by the average value. These characters are governed by a large number of genes. In F_2 segregation, the classification of the phenotype is difficult due to the reason that there are intergrades between the two parental values.

Whether a character is qualitative or quantitative can be decided by actual breeding tests only. When Mendel's results were made known in 1900, inheritance studies in respect of some of the economic characters proved puzzling. The F_2 segregation was not clear cut and in addition to parental forms, intergrades and even forms exceeding the parental limits were found. So it was first surmised that these characters are non-Mendelian in inheritance. Inheritance of height of plants in rice may be discussed here to explain the quantitative variations.

T. 24 is a tall type and T. 282 is a dwarf one. F_1 of the cross between these two types exhibited dominance of tallness. The height frequencies of F_2 plants, when plotted in graph give a definite bimodal curve (Fig. 106). The data are presented in table 65. Counts in 25 segregating F_2 families showed 3554 talls to 1197 shorts which fit in with expectations on monogenic segregation.

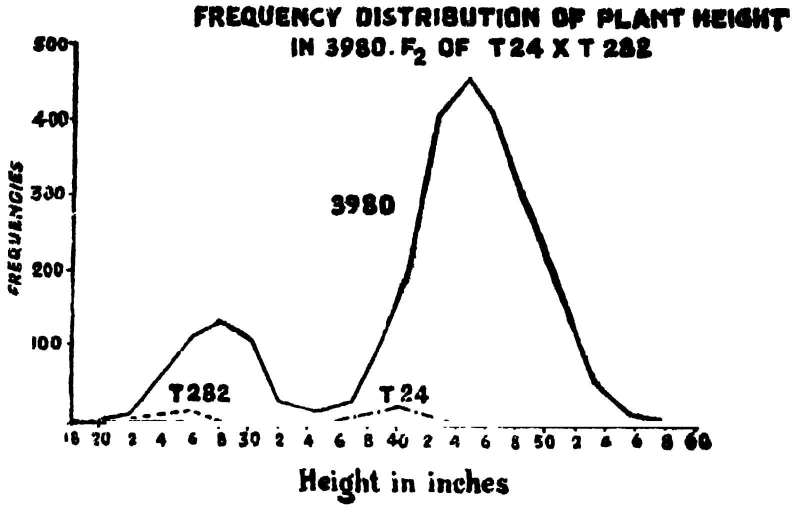

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Fig. 106. Bi-modal curve indicates the segregation of a single pair of mendelian factors.

From the data presented here it is clear that height of rice plant in this cross is governed by a single pair of Mendelian factors. The behaviour of the same character in another cross T.24 × T.280 is in contrast to this. The data pertaining to this cross are presented in table 66, and the same are graphically represented in Fig. 107. The F_1 plants in this cross are as tall as the tall parent.

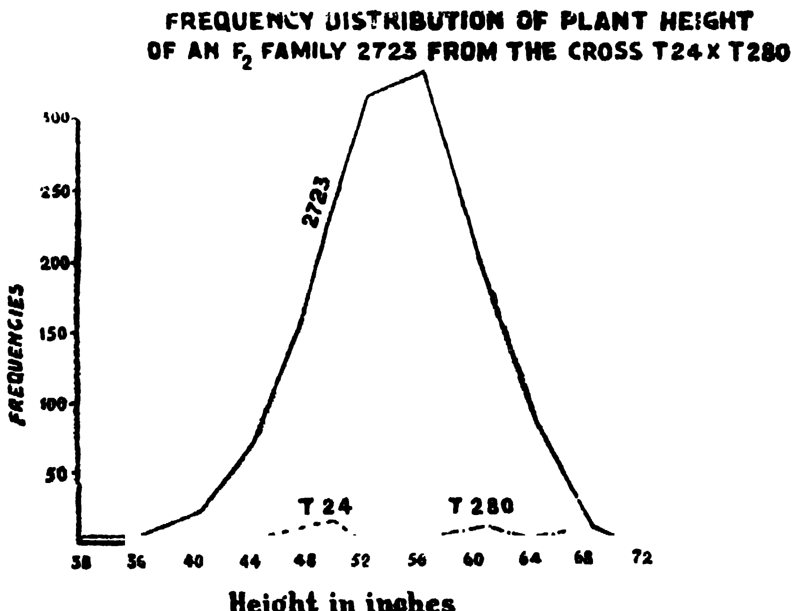

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Fig. 107. Note the single mode of the curve showing that large number of factors are segregating.

TABLE 65.

	Height frequencies (Height in inches).																											Mean Height.
	20	22	24	26	28	30	32	34	36	38	40	42	44	46	48	50	52	54	56	58	60	62	64	66	68	70	72	
Short Parent ...	...	4	9	10	1	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	24·7.
F_2	4	11	60	107	132	88	26	16	26	88	187	392	451	388	275	144	51	15	4	1	...	...	...	...	...	...	...	27·5 for shorts. 44·5 for talls.
Tall Parent ...	...	...	...	...	...	...	...	...	2	11	20	12	1	...	...	...	...	...	...	...	...	...	...	...	...	...	...	40·0.

The height of short parent ranges from 22″ to 28″.

The height of tall parent ranges from 36″ to 44″.

Note that the height of F_2 plants ranges from 20″ to 58″.

TABLE 66.

Height frequencies of F_1's (in inches).

Serial No.	Particulars.	13—16	17—20	21—24	25—28	29—32	33—36	37—40	41—44	45—48	49—52	53—56	57—60	61—64	65—68	69—72	73—76	Mean height.
1	T. 280	...	...	...	...	...	...	...	...	...	...	8	12	...	...	...	...	57·3
	T. 24	...	...	...	...	...	...	8	12	...	...	...	...	...	...	...	...	41·2
	F_1	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	60·0
	F_2 : 2612	...	...	8	13	18	39	121	287	329	235	74	18	6	1	...	...	46·5
	2613	...	6	12	7	14	30	71	185	309	307	149	42	6	...	1	...	48·5
2	T. 280	...	...	...	...	...	...	...	...	...	...	17	3	...	...	...	...	56·0
	T. 24	...	...	...	...	...	...	8	12	...	...	...	...	...	...	...	...	41·2
	F_1	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	58·5
	F_2 : 2616	...	...	4	11	15	27	45	137	264	334	228	85	17	3	...	...	50·2
	2617	...	1	...	3	6	10	25	70	186	297	240	122	39	6	...	...	52·5
3	T. 280	...	...	...	...	...	...	...	...	...	...	1	10	11	1	...	...	61·0
	T. 24	...	...	...	...	...	...	...	...	12	14	...	...	...	...	...	...	48·7
	F_1	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	58·0
	F_2 : 2723	...	...	...	...	2	2	21	70	174	314	336	200	85	10	1	...	54·0

The two parents, T. 280 and T. 24 are quite distinct and their height frequencies do not overlap. In the case of height frequencies of F_2 plants, there is no break and the curve of height frequency distribution is a unimodal curve. The F_1 plants are all fairly uniform but the F_2 shows a great range of variation. This indicates as explained later that the plant height in this cross is controlled by several factors (Fig. 107). As there is no evidence of clear cut 3 : 1 segregation in F_2 such characters could not be explained at first on Mendelian principle. The works of Nilsson-Ehle on the colour of wheat grains showed that the character is governed by three factors with additive effect. On the same basis, inheritance of quantitative characters is explained and therefore the work on inheritance of colour of wheat grains is briefly mentioned below:

In a cross between coloured and non-coloured wheat types, F_1 grains were intermediate in colour. In the case of F_2 population, the intensity of colour of grains fell into three grades, intense, light and very light depending on whether there are three, two or one dominant gene in the respective genotypes. Thus the three factors had individually the same effect but when combined they showed additive effect. It must be noted that the F_1 is intermediate and least variable and in the F_2 each of the pure breeding grand parental type appears in the proportion of 1 in 64. With increase in the number of factors governing a character the proportion in which the parental forms appear

in F_2 is reduced and is given by the ratio 1 : 4n where n represents the number of factors involved. Many of the economic characters such as yield are governed by much larger number of factors and to recover the parental types in sufficient frequency a very large population must be raised. If the F_2 values are plotted against their frequencies as shown in Fig. 107 a curve with a single mode is the result. In the case of segregation for a single pair of factors, the curve is bimodal as shown in Fig. 106. Fisher showed that in the case of characters governed by a large number of factors, the F_2 population is represented by the expansion of the binomial expression $(a-b)^r$ where the powers of '*a*' represent the recessive factors, the powers of '*b*' represent dominant factors, and the coefficient of terms represent the frequencies of each. If 5 pairs of factors are involved, the F_2 population may be represented as shown in table 67.

TABLE 67.

Class.	a^{10}	a^9b	a^8b^2	a^7b^3	a^6b^4	a^5b^5	a^4b^6	a^3b^7	a^2b^8	ab^9	b^{10}
Frequency.	1	10	45	120	210	256	210	120	45	10	1

The frequency on either side of mode, $a^5 b^5$ is equally decreasing and the graph is therefore a normal unimodal curve. The parental form appears once in 1024. *In respect of quantitative characters, the* F_2 *values may be spread between the two parents and there may be no clear cut difference between the parental and varied recombined forms and this is not due to blending of characters, but due to segregation of a large number of genetic factors where the particular genotype is not definitely identifiable with a particular phenotype.*

The cross between two types of chilly studied at Pusa may be cited as an example for quantitative variation. T. 3 bears globose fruits and T. 29 bears elongate fruits. The fruits of F_1 plant were intermediate between the two types and the range of F_2 variation is shown in Fig. 108. The mean length of fruits is shown in table 68.

TABLE 68.

	Mean length of fruits.
T. 3 parent	$2{\cdot}50 \pm 0{\cdot}000$
T. 29 parent	$11{\cdot}02 \pm 0{\cdot}133$
F_1	$5{\cdot}32 \pm 0{\cdot}060$
F_2	$5{\cdot}75 \pm 0{\cdot}037$

Though the mean fruit lengths of F_1 and F_2 generation plants are close to each other, the F_1 values are uniform while the F_2 range is great. The inheritance of such characters is explained on *multiple factor hypothesis.*

2. Types of F_1 and F_2.—The F_1 may represent the average of the two parents or may be inclined towards one of the parents. *Its variability is approximately the same as that of the parents.*

In F_2 the mean value of the population may be the same as in F_1 but its variability both in range and as measured by standard deviation is large.

This range and variability is due to segregation and varied recombined forms (Fig. 108). The F_2 progenies from the different F_1 plants of a cross behave alike, showing that all F_1's are alike in respect of their breeding behaviour.

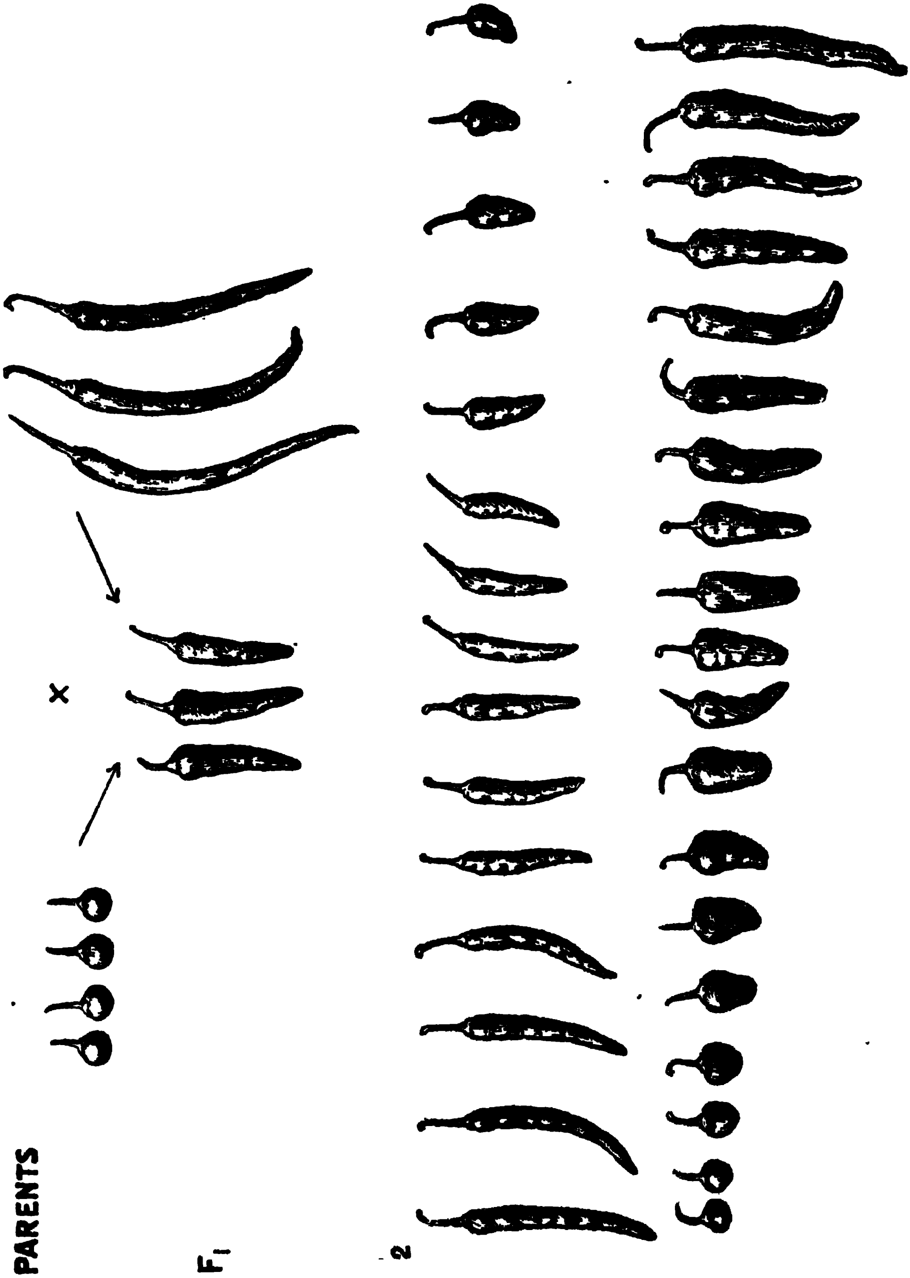


Fig. 108. A cross between T. 3 and T. 29 in chilly (*Capsicum annuum*). Note the uniformity of F_1 and the range of variation in F_2.

(*after Deshpande* 1935).

When F_3 progenies are studied there is difference in mean value and variability in respect of each F_2 family. The variability is smaller in F_3 as compared

to F_2. *In further generations, it is possible to isolate pure breeding types with different values between the parental ones.* This is due to the fact that on selfing, in the course of few generations, the population tends to become homozygous.

If a quantitative character such as height is taken to be governed by five pairs of factors, the parents and F_1 may be represented as shown below :

Parents	...	AABBCCDDEE × aabbccddee.
F_1	...	Aa Bb Cc Dd Ee.
F_2	...	There will appear $2^5 = 32$ phenotypes if dominance is complete in all the factors, and there will be $3^5 = 243$ genotypes.

By selection in further generations, it is possible to isolate genotypes such as :

AA BB CC DD ee
AA BB CC dd ee
AA BB cc dd ee
AA bb cc dd ee and so on,

If it is taken that in a cross, the recessive parent is 30 inches tall and that every dominant factor increases height by 5 inches and that they show cumulative effect, then four recessive factors plus one dominant factor will give 35" tall progeny ; three recessive factors plus two dominant factors will give 40" tall progeny and so on.

This explanation represents the main basis of multiple factor hypothesis. All the factors governing a quantitative character may not individually have equal and identical phenotypic effect but may show differing values. So it is possible that the F_1 may not show the exact mean of the two parents in all cases. This is shown by the data in table 69.

TABLE 69.

RICE.

Flowering duration in days	T. 24	...	100	
	T. 310	...	85	
	F_1	...	86	
Flowering duration in days	T. 24	...	96	
	T. 33	...	96	
	F_1	...	89	Earlier than the two parents.
Flowering duration in days	T. 24	...	96	
	T. 282	...	108	
	F_1	...	100	
Height of plants in inches	T. 24	...	46	
	T. 280	...	60	
	F_1	...	58	
Grain length in mm.	T. 33	...	5·88	
	T. 25	...	7·14	
	F_1	...	6·56	
Grain breadth in mm.	T. 33	...	2·05	
	T. 32	...	2·78	
	F_1	...	2·54	

The interaction between different quantitative genes may result in different types of F_2 variation. In the case of height of rice plants referred to in the preceding section, the F_2 values exceed those of the parents and this is termed *transgressive variation*. The parents show an average height of 57·3" and 41·2"; the height of F_2 plants ranges from 17" to 72". Thus some progenies are shorter than the short parent and some are taller than the tall parent. This type of variation arises in cases where some of the favourable factors are lacking in one or the other parent. If five pairs of factors are assumed to govern the height, the parental genotypes may be represented by AA BB CC DD ee and aa bb cc dd EE and the transgressive forms will then be AA BB CC DD EE and aa bb cc dd ee.

Another interesting instance is a case where the parents are of equal phenotypic value but in F_2 there appears a wide range of variation and homozygous types with different values could be established by selection in future generations. In such cases the two phenotypes of the parents are governed by different genotypes and in the progenies of the cross, variations arise.

If AA BB CC dd ee ff represents the genotypes of one parent and aa bb cc DD EE FF represents the genotype of the other parent their phenotypic effect say height, may be equal. Their genotypes differ in the dominant genes. The F_1 genotype is Aa Bb Cc Dd Ee Ff and in F_2 recombined forms with one to six of the dominant genes appear. The genotype AA BB CC DD EE FF exceeds the parental height because it is governed by all the six dominant genes while any one parent is governed by three dominant genes only. In rice, for example, a cross between two types T.29 and T.102 where the parental heights were 47 and 48 inches respectively, the range in segregating families was from 42 to 68 inches.

In some instances the parental types that appear in F_2 and later generations are not identical with the original parents in respect of the quantitative characters concerned. They show shift in their values. In a cross between round grained *Sirumani* and long grained, *Anaikomban* in rice, F_1 was intermediate and in F_2 there was segregation. Round grained types like Sirumani and long grained types like Anaikomban appeared in F_2 generation. But the mean length of these extracted types were not the same as in the parents. The extracted round grain was little longer, and the extracted long grain was a little shorter than the corresponding parents. This phenomenon is termed *shift*.

There is yet another type of F_2 variation where the two parents entering a cross may differ in respect of a quantitative character and the F_1 may be intermediate. The F_2 also may show the intermediate value without high range of variability. The F_2 values are not spread from one parent to the other but are confined to a narrow range with the mode close to that in F_1. This is not due to blending of characters, but due to the character being governed by a very large number of factors.

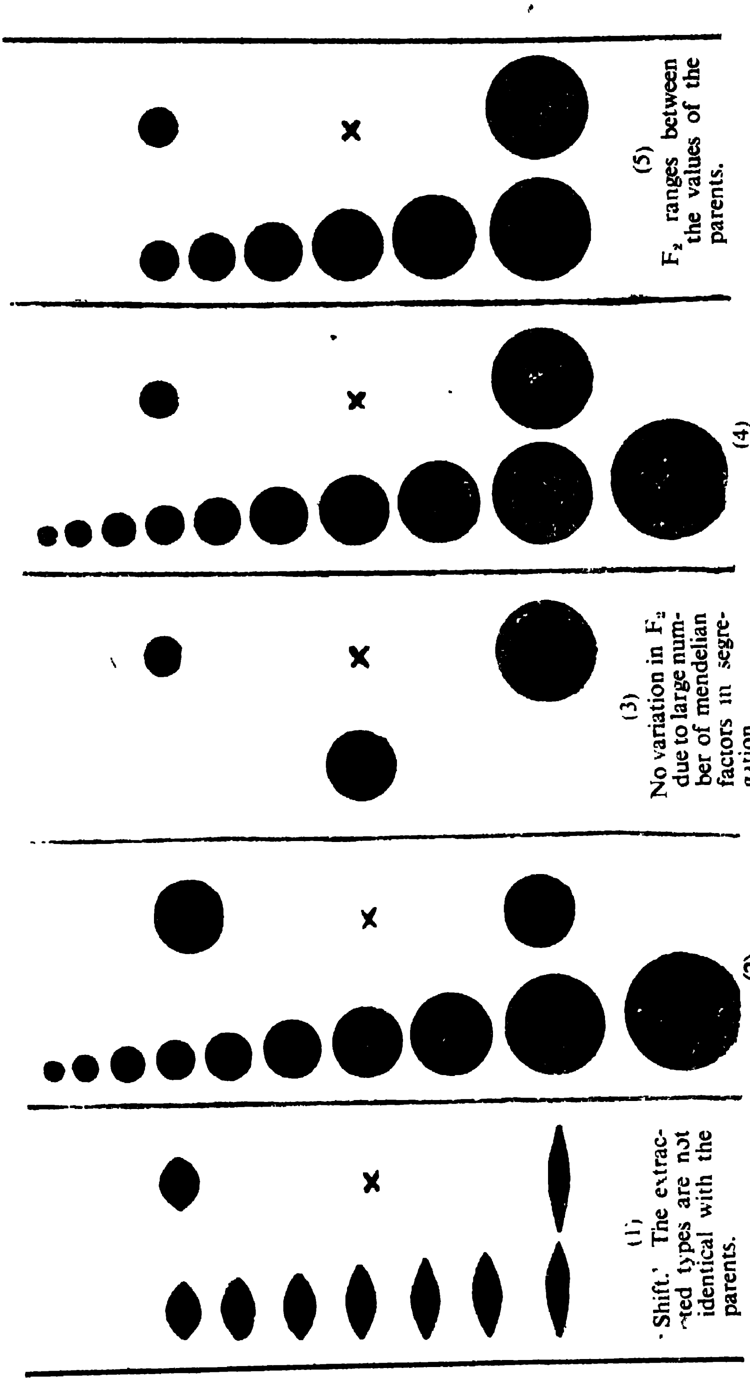


Fig. 109. Diagram to illustrate the types of F_2 variation.

The slopes of the curve plotting F_2 values are gradual, if the number of factors governing the character is few : the slopes are steep if the number of factors is many. When the F_2 does not show high range of variability even though the parents widely differ, it shows that the character is governed by a large number of factors. A very large F_2 population is to be raised in those cases to recover the parental forms, and in many cases it may not be possible to do so for practical considerations. On account of these reasons the F_2 population shows a narrow range of variation around the mode.

3. **Effect and location of multiple factors.**—The complexity of inheritance of quantitative characters is not only due to the character being governed by a large number of factors, but also due to the difference in the effects of the individual genes. Some of the genes may affect the character in plus direction and some may affect it in minus direction. Their individual effects may not be equal but their total effect is additive.

The same character may be governed by multiple factors or by a single factor. In one cross involving the flowering duration in rice, the F_2 segregation was 1 : 2 : 1 of early, intermediate and late types. In another cross, the same character showed segregation for multiple factors. The height of rice plants considered under section 1 of this chapter is another example for such a phenomenon.

In respect of location, all the factors may not be located in the same chromosome but may be distributed in different ones. In *Datura* it was found that the genes affecting height of plant are located in all the 12 chromosomes which represent the haploid number. *It is probably because of such distribution on different chromosomes, that no particular qualitative character is found to be directly associated with the expression of a quantitative character.*

Chapter 15

SELECTION

SELECTION—POPULATION CONSTITUENTS—SCOPE OF SELECTION—ARTIFICIAL VS. NATURAL SELECTION—SELECTION METHODS—PLANT SURVEY—ACCLIMATISATION

1. **Selection.**—Botanists of the eighteenth century interested themselves in the systematic study of variation existing in Nature. There were various attempts at classification of plants. The Linnean system came to be regarded as quite sound and the 'species' of the Linnean concept is now definitely regarded as an important step in evolution. Speculations regarding the origin of the species led Darwin to hypothesise *Natural selection* as a force bringing about such differentiation during evolution. This was mainly based on his keen observations of nature, but there was no method by which it could be experimentally tested, for, at that time the mechanism of inheritance was not definitely known. The re-discovery of Mendel's laws and the subsequent discovery that the chromosomes are the physical basis of heredity, enabled biologists to study variations experimentally. The particulate theory of inheritance gave hopes for recombining the desirable characters into one single individual. In nature, the desirable characters were not all found grouped together in one individual and therefore recombining the desirable ones was the main scheme of breeders. Hitherto, the breeder selected what was found in nature as a result of natural selection or unconscious efforts of man. His skill lay in choosing the best type from the naturally existing populations but the dawn of twentieth century enabled him to plan in creating new forms. The artificial selection by plant breeders produced many useful forms.

The characters, for whose values man selects the particular individual from a mixed population, may have no selection advantage in nature. In other words, the newly selected plant may not prove better than the rest when left to compete in nature. Therefore, a plant breeder may find himself opposed to natural tendencies and hence two problems face him. (1) *The selection of the desirable types,* (2) *Maintenance of the same under cultivation without deterioration in the characters for which selection was made.*

Both these problems of selection are beset with difficulties and the genetic basis of the problem is discussed briefly here.

2. **Population constituents.**—By selection, a new type is not evolved, but the breeder picks out the best individual which may be present in few numbers in a large mixed population and multiplies the selected type. If selection is to be effective, there must be variation in the population. *Selection in a uniform or homozygous population cannot effect improvements.*

The problems of variation were already discussed. Mutation rate is so slow that it is of no significance to a breeder who is aiming at improving the

type within few generations. Further, most of the mutations are deleterious. *Variations due to environment are of agronomic interest and do not form the basis for permanent improvement in the germinal stock.* Therefore, only such variations as are transmitted to the progenies are of importance to the plant breeder. In the case of plants which bear both the sexes in the same individual, there are two aspects of the problem of variation. (1) when the progenies are raised through selfed seeds, (2) when the progenies are raised through out-crossed seeds. In the case of plants which are propagated asexually, the problem of variation is different from the sexually propagated ones.

Indiscriminate crossing between genotypically different individuals, leads to changes in population composition by the acquisition of new or loss of old characters. There are two opposing tendencies within a population. (1) the tendency to conserve the genes (2) the tendency to change. A population which shows stability is only apparently so, but it is really in a state of flux so far as genotype is concerned.

If in a population the factors A-a occur in the proportion m_1 and n_1, and if there is free mating among the individuals, it can be mathematically shown that the composition of the population in respect to this factor pair is $(m_1A+n_1a)^2$. Similar is the case in respect of all other factors and the total composition of the population is represented by the continued product of the various expressions.

$$(m_1^2AA+2m_1n_1Aa+n_1^2aa)\quad(m_2^2BB+2m_2n_2Bb+n_2^2bb)\quad(m_3^2CC+2m_3n_3Cc+n_3^2cc).$$

In this case the population is obviously highly heterozygous. The case is different in self-fertilised plants. In these latter, the factors are distributed as follows :

$$(m_1AA+n_1aa)\quad(m_2BB+n_2bb)\quad(m_3CC+n_3cc).$$

The cross fertilised crops are termed *allogamous* and the self-fertilised crops are termed *autogamous*. In nature, many crops show both types of pollination in varying proportions. *Where autogamous reproduction is the rule, the population consists of mixtures of homozygotes which on single-plant selection yield quick results.* Though on theoretical considerations the number of pure types that may occur in an autogamous population is large, actually, only a few occur due to the elimination of a large number of them in nature.

In allogamous species, the number of possible recombinations is large, but due to linkage which is wide-spread, this theoretical number is much reduced. Elimination of various combinations due to lethal factors, etc. is also large. Therefore in allogamous species also the variability is far less than the theoretical one. In this case, selection shows continued improvement over long period and the theoretical limit is reached when the selected population is *homozygous and homogeneous*. This latter process is very much hastened if the selection follows selfing in the population.

Similarly, if *mass selection* is practised on self-fertilised crops, the final limits of selection are never reached for the reason that single pure line is never established and the mass selected bulk will consist year after year not of the same set of pure lines but of different sets of pure lines thus giving continuous results of selection.

The basic principles underlying these selections are explained on the basis of Mendelian laws of inheritance. Mass selection and even hybridisation were practised in early times for crop improvement without the knowledge of the basic principles.

3. Scope of selection.—Selection for improved types of economic plants is in progress in various research stations. In some instances the work has been in progress for over four decades and more. The question therefore arises " What is the scope for selection ? Can unlimited changes by artificial selection be produced in the existing types of plants ? "

It has been pointed out that variation is of two kinds (1) environmental and (2) genetic. The genetic variation which is only heritable can be evaluated by measuring the phenotypes which may also be affected by environment. Fluctuating variations are to be accounted for in estimating the genetic variability of a population.

Naturally existing populations are not homogeneous. Even in the case of plants which are self-fertilised over a large number of generations, heterogeneity can still be demonstrated. *Therefore the scope of selection will depend upon the heterogeneity and the range of variation in the foundation stock. If the foundation stock is homogeneous and consists of Homozygous types, there can be no genetic variability without hybridisation. Therefore selection cannot show any improvement. Castle's experiments on rats and Payne's experiments on Drosophila are of interest in this connection.*

Hooded pattern in rats is a simple recessive to Irish pattern. The hooded pattern was variable in extent ; in some cases it confined to the head only and in others it extended a little further to the back in stripes of different width. On the foundation stock, selection was made in two directions : (1) in the plus direction to increase the hood (2) in the minus direction to eliminate it. The selection was effective in both the directions. The results were first interpreted on the assumption that the factors for hoodedness can be changed to h^1, h^2, h^3 . . . . h^n by selection and that this change brings about the increase or decrease in the hood pattern. Later experiments showed this explanation to be wrong and that the experiment can well be explained on multiple factor hypothesis. The foundation stock being heterogeneous for these factors, selection was effective in sorting out the different types. Selection in this case did not operate directly in increasing or decreasing the pattern.

Experiments of Payne were on the number of bristles on the scutellum of *D. melanogaster*. On an average there were 4 bristles. 2,861 flies were counted and 99.5 per cent showed 4 bristles. By selecting a pair with 4 and 5 bristles as foundation stock, experiments were conducted by mating brother and sister

and selecting for increase in the number of bristles. The behaviour of F_1 and F_2 showed very little evidence of heterozygosity. Selection in further generations was effective and there were increased number and range of variations.

Payne explained this assuming that two to three mutations occurred in the course of the experiment. If this be true the observed mutation rate must be far in excess of the usual one observed in nature. Further, mutations in the direction of selection are rare. Goodale, discussing the effects of selection, concludes " breeders need not hesitate to attempt the improvement of any character which in his judgment needs improvement ; even the slight variation in the character seems to offer a little scope." " It is immaterial whether that which is developed by selection was hidden in the germ cells of these individuals with which the experiments began or whether it is a new creation."

In maize, selection was made at the Illinois station for increasing the oil and protein contents. In the foundation stock of Burr's white corn individual ears were analysed for these contents. Protein content ranged from 8 to 14 per cent with an average of 10.93 and the oil contents ranged from 3.8 to 6.0 per cent with an average of 4.69 per cent. Selection was practised both in the plus and minus directions. In the case of proteins the plus line moved up to 15 per cent average content and in the minus direction it moved down to 7.5 per cent average content. In the case of oil content the plus line moved up to 9.35 per cent average and the minus line moved down to 1.87 per cent average content. The above results were obtained after 23 years of selection at the end of which period *there was no evidence that the upper or lower limits were reached.*

In the above experiment pollination was not controlled. *Therefore, there was heterozygosity even after* 23 *years of selection.* Later experiments by East and Jones showed that selection effect is rapid in self-fertilised lines. After 5 years, as high as 17.07 per cent protein content was reached as against the 15.66 per cent reached after 23 years in open pollinated line. Selfed lines were poor in vigour but more vigorous lines were bred by crossing two high-protein selfed-lines and by this method high protein content was retained and the vigour increased.

These experiments point to the fact that in the case of characters governed by multiple factors, improvement can be effected by rendering favourable factors homozygous or by recombining them from different homozygous selfed lines.

The work of Mather on *Drosophila* which is discussed in detail in chapter XX explains the possibilities for variations to arise in homozygous and heterozygous populations. An individual can store small or large potentialities for changes in genotype by the two types of balancing the plus and minus genes. (*Vide* chapter XX).

4. Artificial *Vs.* Natural selection.—In selecting improved types, the plant breeder is artificially developing certain characteristics in the plants. He is

keen on the economic characters only, and his selection is based on measurements of such characters. Very often, other characters which may be linked with them are not taken into account. Within the short period of experimentation in Research Farms, there is neither the time nor the scope to study the advantages of the new characteristics under Natural Selection. Many instances have been met with, where the breeder failed because he attempted in a direction opposed to natural tendencies. The crop census studies carried out at Indore, revealed that the failure of Jarilla, a verum type in Malwa, is due to such causes. This problem is further discussed in a later chapter.

5. Selection methods.—In pre-Mendelian periods, the best plants or *elites* of the population were selected at the time of harvest and the seeds from the same were preserved for sowing in the next season. This is termed *Mass selection.* This has been primarily the method by which improved types were evolved in the earliest days of history of plant breeding. In selecting improved types of crop plants, there are three primary considerations for a plant breeder : (1) the breeding behaviour of the crop indicates whether it is homozygous or heterozygous, (2) the mode of propagation, *viz.*, sexual or asexual, (3) Exotic or indigenous nature of the crop. In self-fertilised crops the tendency is towards homozygosity and in cross-fertilised crops the tendency is towards heterozygosity. *In either case, mass selection is concerned with the phenotype at the time of selection and it ignores the breeding behaviour of the selected type in future generations.* When seeds from a large number of selected plants are mixed together, the crop raised from such a seed lot may be not only *heterogeneous* but also *heterozygous.* Therefore improvement in crops by mass selection is short-lived in its benefit and must be practised every season. This is especially the case in crops which are cross-fertilised in nature.

All recent methods in crop improvement are mainly based on genetic considerations. Some of the points in relation to selection were outlined already. The first step is to explore the possibility of selecting a naturally existing type with all desirable qualities and multiply the same. Such a type may be existent in the same locality or it may be found in other parts of the world. In the latter case it must be introduced into the tract and studied for its behaviour in the new environment. *If such naturally existent types are not available then the plant breeder has to create artificially higher ranges of variation by hybridisation.* From the hybrid progenies, desirable types are selected. The main difference between the selection in the naturally existent types and the selection in the hybrid progenies of an artificial cross, is that the former has already gone through natural selection and hence is comparatively stable while the latter may yet be unbalanced.

It has been already pointed out that the breeding behaviour of a crop depends upon the pollination methods. If the crop is self-fertilised then the population will be homozygous; if it is cross-fertilised it will be heterozygous. Since many crops are subjected to both the types of pollination to varying degrees, homozygosity or heterozygosity in the population will also vary accordingly. If the character under selection is to be of permanent value

then the population must be rendered homozygous to prevent segregation and deterioration. If there is cross-pollination to any degree at all, the whole population must be subjected to controlled pollination.

The case of asexually propagated crops is different from that of sexually propagated ones in that the former can be multiplied without permitting heterozygous factors segregating. *This prevention of segregation of heterozygous factors results in homogeneity of the population though they may be heterozygous.* These plants have potentialities to throw large variations if they are propagated sexually. Therefore, in the case of asexually propagated crops, the population shows very little variation. Variations can be induced by subjecting the crop to sexual propagation until desirable types are thrown out. The selected types are then asexually propagated ;

The crop plants may be grouped as shown below :

I. Indigenous in origin and under cultivation since ancient times :

A. Sexually propagated.

(i) self-pollinated.

(ii) cross-pollinated.

(iii) self and cross-pollinated to varying degrees.

B. Asexually propagated.

II. Exotic in origin and recently introduced into cultivation.

A. Sexually propagated.

(i) self-pollinated.

(ii) cross-pollinated.

(iii) self and cross-pollinated to varying degrees.

B. Asexually propagated.

The consideration whether the plants are indigenous or exotic provides a clue to the extent of variability in the locality. If a crop is under cultivation since hundreds of years in the tract, it is generally characterised by the existence of a large number of agricultural varieties, *e.g.*, cholam, though of African origin, has been under cultivation in this country for some centuries and there are a large number of varieties under cultivation in different tracts. These agricultural varieties differ from one another in many respects and show wide variations in many of the economic characters. According to Vavilov's findings the variations are largest in the ancient centres of origin and therefore an exploration of Africa will reveal large variations not met with in this country. The primary and secondary centres of origin, then provide the best places for exploring variable types. This has been done in many crops like wheat, rye, barley and potato. Russian botanists discovered valuable characteristics not found even in their vast country. These plants could either be directly introduced into cultivation or if they fail in that, they are used as parents in hybridisation programme and the valuable characteristics are transferred to the local types.

With the foregoing general considerations in back ground, the field technique in selection may be classified as follows :—

(1) Plant survey and Acclimatisation.

(2) Mass selection.

(3) Pure line selection.

(4) Clonal selection.

(5) Hybridisation and selection.

These are further discussed in the following pages.

6. Plant survey.—That survey of plant resources is an important preliminary step in any plant breeding programme has been mentioned. The immense importance of this was not realised until recently. World expeditions were organised by the Russian botanist Vavilov and all agricultural varieties and wild plants allied to the cultivated ones were all gathered. These expeditionists deviated from the old practice of collecting and drying the plants for Herbarium reference. They collected live plants and raised them in Russia under suitable environments. Over 200 crop plants and a total of 150,000 specimens were collected. Roughly the number of samples collected for some of the crops is indicated below :

Wheat	...	29,200	Maize	...	9,000
Barley	...	13,000	Beans	...	20,000
Oats	...	9,000	Potatoes	...	1,000

From the study of these world collections, Vavilov enunciated two basic principles of great importance to plant breeders : viz., *law of homologous series in variation* and the hypothesis on the *origin of cultivated plants.*

More than 2,000 scientific and research workers were engaged in this work in Russia and about 168 million roubles were spent every year prior to World War II. There are 1,233 agricultural stations of which 646 are for plant industry. These facts are mentioned to show that enormous organisation is required for the world survey of agricultural plants. The Russian survey is by no means complete. China, Indo-China, Hindustan, Arabia, South Africa, Uganda, and Brazil are some of the places not yet surveyed by them. The vast survey was not without its benefits to the country. Many valuable new species were discovered, new crop plants selected and new characteristics introduced. Vast strides in agricultural progress were made. Some of the important findings are mentioned here as examples.

Wheat.—This crop is shown to be of high ecological specialisation and exceptional polymorphism. It is of great plasticity and adaptability but direct introduction was not successful. Two endemic new species were discovered :

Triticum persicum : endemic in Transcaucasia.

T. timopheevii : endemic for Georgia.

Barley.—The cultivated barleys of the following countries are of interest with reference to their important characteristics.

(1) ARABIA : Earliest, most drought resistant, large grains and relatively high yield.

(2) ASIA MINOR : Strong straw, large grain, relatively drought resistant and productive.

(3) ABYSSINIA : Large grain, strong straw, relatively productive even in northern latitude, grains of good malting quality in White Russia.

(4) MEDITERRANEAN : large grain and drought resistant.

(5) SYRIA AND PALESTINE : large grains, resistant to drought and fungus diseases.

(6) CHINA : early, naked grains, strong straw and adaptation to northern conditions.

(7) INDIA : early, strong straw, almost round grains.

(8) AFGHANISTAN : early, drought resistant and grain of good shape.

315 types were collected and tested in 25 stations. From the view of extending barley cultivation northward, types from China, Abyssinia and Arabia are useful ; and for malting, types from Abyssinia and Asia-minor ; and for dry regions types from Arabia are important.

Potato.—Prior to this survey only one species, viz., *Solanum tuberosum* was known under cultivation. The survey revealed 14 species under cultivation. Wild species in large numbers were collected. *S. acaule*, stemless potato growing in mountains of Peru and Bolivia upto an altitude of 5,000 meters near to snow line was discovered. It is highly cold resistant. Mexican species, *S. antipoviczi* is *Phytophthora* resistant and *S. demissum* is resistant to this fungus and frost. The survey by Russian Botanists was so useful that Americans sent an expedition in 1932 to the same regions.

The expedition not only revealed new forms of cultivated species of crop plants, but also revealed substitute plants. 992 fibre plants were collected. *Triumfetta*, *Althaea*, *Crotalaria*, *Sesbania*, *Desmodium*, *Genista* and many others are tried as fibre plants.

The importance of a thorough survey of at least the tract for which breeding programme is drawn up cannot be over-emphasised. A type, which meets the requirements of the plant breeder may be existent mixed up in the local bulk. Attempts to isolate such types will bear greater fruit than those to evolve a new one by artificial hybridisation and selection.

7. Acclimatisation.—A general study of the quality and yield of different crops in different region will reveal that they are all not uniform in all places.

They may be superior in one place and inferior in another. Therefore, introduction of superior types from neighbouring or distant regions has been frequently practised. Coffee, Tea, Potato, Tobacco, Cambodia cotton and groundnut are some of the newly introduced crops of India. Sometimes even in the first year of introduction, the introduced crop grows successfully and establishes itself in the new tract. It may even grow better in its new home than in its old one. Thus, groundnut and Cambodia cotton have established themselves in S. India and are now raised in large acres. Attempts to introduce Sea Island and Egyptian cottons in India have so far failed.

There are many crops which have been introduced in this country in the distant past. Chilly, Pumpkin and Squashes, Sorghums, Castor, etc., are examples. The introduced plants may not thrive well in the first few seasons but later they may establish themselves well. This was first taken as a proof for the inheritance of acquired characters. It has been shown in an earlier chapter that acquired characters are not inherited. *Therefore acclimatisation must be explained on the basis of selection of new genotypes.* The possibilities are (1) the original bulk which is introduced in the tract may not be truly homozygous and hence there is already genotypic variation, expressed or potent (2) small micromutations in various genes may take place (3) new type of balancing between the polygenes may give rise to variations. These changes may not always be in the desired directions, for the introduced type may improve in the course of first few years or break down in that period. The introduction and acclimatisation of the New World cultivated cottons are of interest in this connection. Tanguis cotton, a jassid resistant American type was introduced in the Punjab. It was successful in the first few years but later it broke down. Similarly, American cottons, introduced in China were successful in the first few years but later they broke down. The reverse of this process is also possible. The introduced type may be poor in the first few years but after 4—5 years may excel the local. Co_2 cotton when introduced in Gambia (W. Africa) excelled local types after 5 generations.

If acclimatisation is to be successful, the introduced bulk must possess genetic variability. A truly homozygous type with very little of expressed or potent variability, is either successful in the first instance or not at all. In such a case there can be no gradual adaptation to the new tract. The introduction of American cottons in India is an example of acclimatisation. The bulks introduced in early periods were unselected bulks and therefore they possessed genetic variability. By acclimatisation, genotypes suited to the local environment could be selected and thus the acclimatisation proved successful. Recent import of improved seed material from those countries proved a failure, for the reason that the recent seed stocks were pure lines possessing very little of genetic variability. *Therefore, if acclimatisation is sought, unselected bulk must be the starting point instead of pure lines.*

There is however, one important consideration in this respect *viz.*, a breeder's pure line is never truly homozygous on theoretical considerations. The number of factors governing an economic character is so large as also the number of economic characters of importance that pure line selection

must be carried over a large series of years before true homozygosity is reached. A breeder never carries his experiments to this level of perfection on various considerations to be discussed later. When the selected material reaches a particular level of purity, he releases it as an improved strain. Where such material possesses desirable genotypes for the new locality, selection in another breeder's material may prove useful. There are a number of instances where improved strains of cotton not showing variability in its original home of selection, has been improved further by introduction in a new area. *The possibilities of success of acclimatising a breeder's material fall into two classes* (1) *by selection of new genotypes* (2) *by place effect.*

Success in acclimatisation by selection of new genotypes has been already discussed. As examples, may be mentioned U4 of Africa and 289 F of the Punjab which have given rise to a number of substrains suitable to different climatic conditions in other regions.

Place effect has been already referred to in Chapter VIII. It is only a variation in the expression of a gene due to different environmental conditions. Harland gives an instance where V 135 Sea Island cotton changed its habit when introduced in Sudan and produced short coarse fibres in Teneriffa. But on re-introduction into its original home of St. Vincent, it behaved exactly like the original stock. The change in phenotype was only due to the changed expression of the same gene in the new environment. An intra-specific hybrid rejected at Coimbatore Cotton Breeding Station proved valuable when introduced in French West Africa. Similarly, Sanguineum 12 of Lyallpur proved to be very late over a period of 12 years but it proved earliest at Rawalpindi. When re-introduced in the former locality it again proved late. Therefore it is evident that acclimatisation is successful either due to place effect or to selection of new genotypes and *not by the accumulation of new factors created by the directive influence of environment.*

Chapter 16

PURE-LINE SELECTION

JOHANNSEN'S EXPERIMENTS—GENETIC SIGNIFICANCE—EFFECT OF SELFING CROSS-POLLINATED CROPS—PRIMARY AND SECONDARY SELECTIONS—BULK FOR SELECTION—FIELD TECHNIQUE—LIMITATIONS—ACHIEVEMENTS

1. Johannsen's experiments.—Measurements in respect of any quantitative character in a population shows variation. A plant breeder selects the plus variations in characters of economic importance. In doing so, one must be certain that the variations in the populations are heritable. Especially in the case of quantitative characters, fluctuations due to environment are large and therefore the breeder has first to assess as to what part of the observed variation is due to genotype and what part is due to environmental influences. Johannsen's (1903) experiments were the first to be designed for the purpose. He studied the weight of bean seed. The seeds in unselected bulk showed wide variations in weight. It was also found that when a bean seed of particular weight is sown, the seeds of the progeny show variation in their weights. Therefore the average weight of the progenies was compared with that of the parent seed. In the first few years of the experiment, heavier seeds produced progenies whose average weight of seeds was heavier and the lighter seeds produced progenies with lighter seeds. After some time, it was found that there was no progress and there was close approximation between the weight of the parent seed and the progeny mean. Still the latter showed variation but within narrow limits and selection in this small variation did not have any effect. By such a process of selection Johannsen established 19 cultures or *pure lines*. *A pure line is a group of descendants selected among the progeny of a single genetically pure self-fertilised individual.* Each of the 19 pure lines selected by Johannsen showed small fluctuating variation and the mean weight of each pure line was distinct from the others. The data of Johannsen are summarised in table 70.

Taking the pure line 15 as an example it is seen that parent beans with 20, 50 and 60 cgm weight produce progenies with the average weight of 46.9, 44.6 and 45.0 gms. respectively. Thus, within a pure line there is small fluctuation which is purely developmental. Any further selection in these is of no effect. This was further confirmed by selecting the *plus* and *minus*

TABLE 70.

Pure line number.	Weight in cgms. of mother beans.						Mean weight of pure line.
	20	30	40	50	60	70	
1 ...	..	...	...	...	63·1	64·9	64·2
2 ...	...	...	57·2	54·9	56·5	55·5	55·8
3 ...	...	...	...	56·4	56·6	54·4	55·4
4 ...	...	...	...	54·2	53·6	56·6	54·8
5 ...	...	...	52·8	49·2	...	50·2	51·2
6 ...	...	53·5	50·8	...	42·5	...	50·6
7 ...	45·9	...	49·5	...	48·2	...	49·2
8 ...	...	49·0	49·1	47·5	...	...	48·9
9 ...	...	48·5	...	47·9	...	...	48·2
10 ...	...	42·1	46·7	46·9	...	...	46·5
11 ...	...	45·2	45·4	46·2	...	...	45·5
12 ...	49·6	...	...	45·1	45·8	...	45·4
13 ...	...	47·5	45·0	45·1	45·8	...	45·4
14 ...	...	45·4	46·9	...	42·8	...	45·3
15 ...	46·9	...	...	44·6	45·0	...	45·0
16 ...	...	45·9	44·1	41·0	...	...	44·6
17 ...	44·0	...	42·4	...	...	...	42·8
18 ...	41·0	40·7	40·8	...	...	...	40·8
19 ...	...	35·8	34·8	...	...	...	35·1

variants for 6 generations to find out the effect of selection. The data pertaining to pure line 19 are presented in table 71.

TABLE 71.

Generations.	Mean weight of mother beans.		Difference between —and +	Mean weight of progeny seeds.		Difference between —and +
	minus.	*plus.*		*minus.*	*plus.*	
(1)	(2)	(3)	(4)	(5)	(6)	(7)
1	30	40	10	35·83 ± 0·44	34·78 ± 0·38	1·05 ± 0·58
2	25	42	17	40·21 ± 0·65	41·02 ± 0·43	0·81 ± 0·78
3	31	43	12	31·39 ± 0·29	32·64 ± 0·21	1·25 ± 0·36
4	27	39	12	38·26 ± 0·16	39·15 ± 0·17	0·89 ± 0·23
5	20	46	16	37·92 ± 0·22	39·87 ± 0·16	1·95 ± 0·27
6	24	47	23	37·36 ± 0·30	36·95 ± 0·21	0·41 ± 0·37

Even when the parent beans show differences as represented in the column 4 of the table, these differences are not reflected in the progenies as shown in column 7. Starting from the unselected bulk, selection is effective in the first few years but later it is not. It is clear from the experiment that the original bulk consisted of mixtures of pure lines. (Figs. 110 & 111). In the first few years, these pure lines were isolated by selection but once the pure lines were isolated, there can be no further effect of selection. The variability within a pure line is merely developmental and fluctuating and is not based on genetic differences.

$$Aa$$
$$1AA + 2Aa + 1aa$$
$$AA \qquad AA + 2Aa + aa \qquad aa$$
$$AA \qquad AA \qquad AA + 2Aa + aa \qquad aa \qquad aa$$

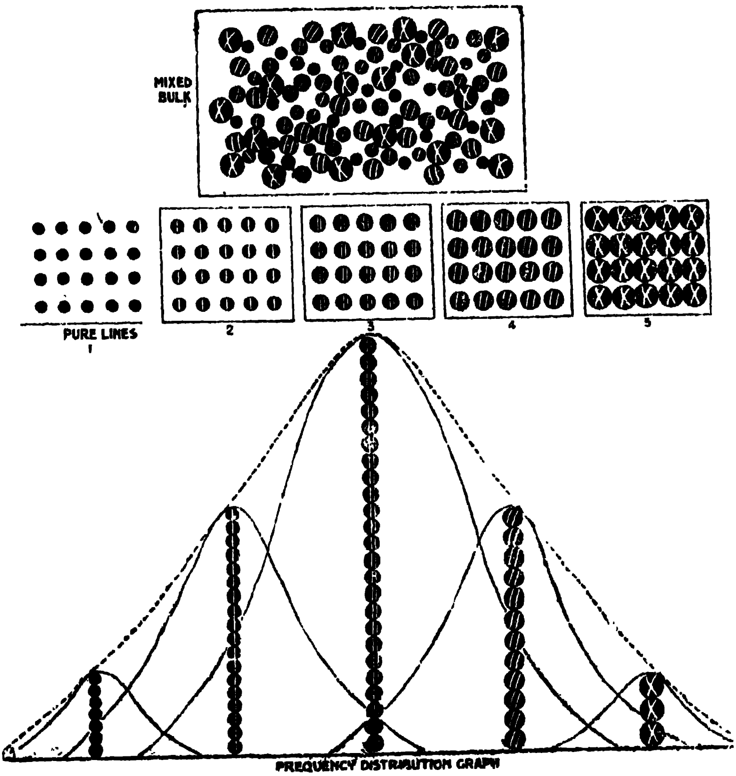


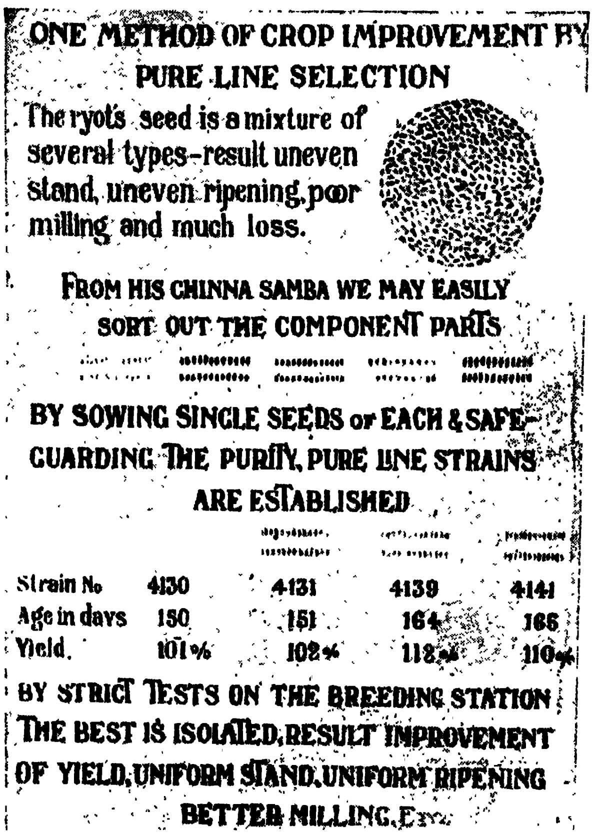
Fig. 110. The bulk crop in a ryot's field is a mixture of types. In a self-fertilised crop, the population can be sorted out into homozygous types as shown in the second row. The frequency distribution for the entire population is shown by dotted lines. This really comprises the frequency distribution of the different pure lines.

2. Genetic significance.—Johannsen's experiments showed that a pure line is without genetic variability, *i.e.*, it is homozygous. When two homozygous types get crossed in nature, and if further out-crossings are prevented, the tendency in selfed population is represented by segregation, *e.g.*, a heterozygote Aa :

On continued self-fertilisation, by the segregation of the heterozygote, more and more of homozygotes are thrown out and the proportion of heterozygotes falls low. This is represented by the mathematical equation :

$$AA = \frac{2n-1}{2n+1}\ ;\quad Aa = \frac{1}{2n}\ ;\ aa = \frac{2n-1}{2n+1}$$

where n represents the number of generations of selfing. In a quantitative character, all the pairs of factors follow the same tendency in their reduction to homozygosity. From this it follows that self-fertilisation renders the population homozygous though it may be heterogeneous in the sense that there may be a number of homozygous types, AA and aa, mixed together. Bean is a naturally self-fertilised crop and therefore the bulk material in which Johannsen started selection represents a population which is *homozygous but heterogeneous* with 19 pure lines and the heterogeneity is eliminated by



(*Photo from Paddy Specialist.*)

Fig. 111. Pure line selection.

pure line selection. While the self-fertilised crops show homozygous groups in nature, the case is different with cross-fertilised crops like pearl millet or

maize. In any group of natural population there is a high proportion of heterozygotes and therefore, pure line selection in these must follow self-fertilisation over a period of years to render the population homozygous.

3. Effect of selfing cross-pollinated crops.—Since pure line selection aims at isolation of homozygous types, this is obviously not possible in naturally cross-fertilised crops without first rendering the latter homozygous by artificial selfing.

The following types of plants are normally cross-fertilised :—

(1) Hermaphrodite flowers with floral mechanism favouring cross-fertilisation, *e.g.*, cabbage.

(2) Self-sterility even in hermaphrodite flowers *e.g.*, some sugarcane varieties ; potato varieties, sunflower and some members of *Crucifereae*.

(3) Uni-sexual and hermaphrodite flowers on the same plant but cross-fertilisation is favoured, *e.g.*, Citrus, grapes, cumbu.

(4) Monœcious plants with cross-fertilisation, *e.g.*, maize, pumpkin, cucumber.

(5) Diœcious plants where cross-fertilisation is the rule. Date palm, hemp, Palmyra etc.

In many cases, such as in sugarcane, fertility may be susceptible to environmental conditions.

Experiments carried out on maize which is cross-fertilised, showed interesting consequences of selfing cross-fertilised crops. In maize, the male flowers are in tassel and the female flowers in cobs. The process of selfing consists in the collection of pollen from the tassel and applying it to the " silk " of the cobs in the same plant, and necessary precautions are taken to prevent contaminations by foreign pollen.

Maize is the only plant where the effects of selfing have been extensively studied. This crop is heterozygous for many characters and there are many distinct commercial types with good yielding capacity. From a single commercial type a number of distinct homozygous types can be selected by selfing, *but selfing leads to deterioration in yield and vigour. These selfed progenies are poor in vigour and yield and are distinct from each other in many morphological characters. One striking feature of selfing is that in the early stages, a large number of abnormalities appeared but later, their appearance decreased in frequency and the selfed line soon reached an equilibrium when it bred pure.* The abnormalities are : albinos, abnormal seedlings, seed germination without roots, dwarfs, fasciation in floral parts, etc. The abnormalities appear due to the fact that some of the deleterious factors which are in heterozygous state in the cross-fertilised population are rendered homozygous on selfing and in the absence of dominant allelomorphs are free to act deleteriously. It has been found that selfing for 10 generations is sufficient to render the crop homozygous. The extent to which the abnormalities appear depend upon the extent of cross-fertilisation and heterozygosity of the natural population.

On theoretical grounds it must be expected that there should be a perfectly balanced type existing in Nature which on selfing should yield superior types. As has been pointed out, the number of factors governing a character and the number of characters making up the plant are large enough to render the appearance of such a genotype rare in the small population at the hands of a breeder. A very large number of plants, possibly some millions may reveal such genotypes. In maize, Collins (1927) isolated a superior type by inbreeding. But the scope of selecting such inbred pure lines is generally rare. *Therefore the value of pure lines in the cross-fertilised crops lies in their utility as parents in hybridisation*, and this is discussed in Chapter XIX.

4. Primary and Secondary selections.—The selection work of Johannsen was carried out on Princess bean which is a self-fertilised crop. On account of the reason that it is a self-fertilised crop, the naturally existing commercial varieties are fairly homozygous for most of the characters. In most of our crop plants such as rice, cholam, cotton, etc., there is always a small percentage of cross-fertilisation in nature. Pure-line selection in these crops is carried out judging the variability in respect of one or two characters only, chief of which is yield. Further, the breeder in the course of his selection, concentrates on few characters only and purity in respect of many other characters is not aimed at. The field technique to be described later is such that a strain is evolved in 7–8 years and as such selfing is not continued over long periods prior to selection. It has been pointed out that in cross-fertilised crops, selfing over a period of 10 years renders the population fairly homozygous but much longer period is necessary to attain a high degree of perfection and the theoretical standard can possibly never be attained at all. Therefore, the improved strain released by straight selection in the local bulk, which is termed *primary selection,* may in some cases still show variability. To meet the immediate demand in the tract, the primary selection may be satisfactory. It is later for consideration whether secondary selection will be successful.

Before resorting to secondary selection an important point to be considered is whether there are no fresh sources of unselected bulk. The improvement that can be expected by secondary selection is naturally, small, because, all large variations have been tapped in the course of primary selection. If local bulk materials with large variations are not available, then secondary selection may be resorted to, as even a small improvement by that means is valuable to a breeder. Tests at Coimbatore in respect of a pure line in rice showed that secondary selection in respect of yield was a failure. But secondary selection has been successful in cotton. K·1 is a secondary selection from a pure line. The success of secondary selection depends upon the presence of genetic variability in the primary selection. This variability can be expected in such of the characters as are governed by a large number of factors as is the case with ginning percentage or lint length of cotton. Secondary selection must be stringently practised at a time when disease or drought is widely prevalent, as, during such seasons, inferior genotypes are naturally eliminated.

The utility or otherwise of secondary selection was recently discussed. *The cotton breeders in India are of opinion that in the case of G. arboreum,*

for which India has more than one secondary centre of origin, selection in natural population is expected to yield large advantages and as such primary importance must be attached to the same.

Residual genetic variation in a primary selection may be expected in such cases where the selection technique adopted in primary selection is not fine enough to detect small variations. In other words, faulty technique may result in residual genetic variability in them. It must be remembered that with the application of statistics to plant breeding, finer and more sensitive field technique are being devised to detect even small variations in populations. If such methods are adopted, the chances for variability in the selected materials are small. As an example may be mentioned the Progeny row-test which when applied to cotton and cholam at Indore could detect small variations in primary selections. The details of this field technique are discussed in Chapter XXV.

5. Bulk for selection.—Economy in respect of time and energy is to be aimed at by a breeder. This could be achieved by efficient technique of selection and the choice of proper bulk material as the basis for selection. The unselected bulk must possess large variations and in such cases selection yields large advantages in short period. Therefore, a plant breeder must first collect bulk samples from different tracts and study the same for the presence of any useful type. Large samples from as many representative tracts as possible are first to be surveyed.

There are certain crops where a large number of agricultural varieties are already under cultivation by ryots and there are others where there are only very few. Taking groundnut as an example, which has been recently introduced into India, there are not many varieties or variations ; whereas in the case of rice there are a few hundreds of varieties which differ from tract to tract. Therefore, large number of variations may be expected in such of the crops as have been under cultivation in the region for a long time and the recently introduced crops show very little such variations. This is to be naturally expected for the reason that any variation now present in an introduced crop is that derived from the small bulk of seed first imported into the country and the crop has not been under cultivation for sufficiently long period to give rise to new variations by the various genetical phenomena hitherto considered. In the places of origin, such as India for some crops, greater attention must be paid to primary selections. Only in such of the crops as groundnut, coffee, etc., selection from fresh introductions is to be sought. To give an example, groundnut was first introduced in Madras State at about 1850 ; further improvement was made by fresh import of the variety " Mauritius " from Mozambique in 1898. From that year fresh imports of varieties from other countries were continued and in the year 1930, Saloum (A.H. 25) was introduced and this excelled the local bulks by 25% in yield.

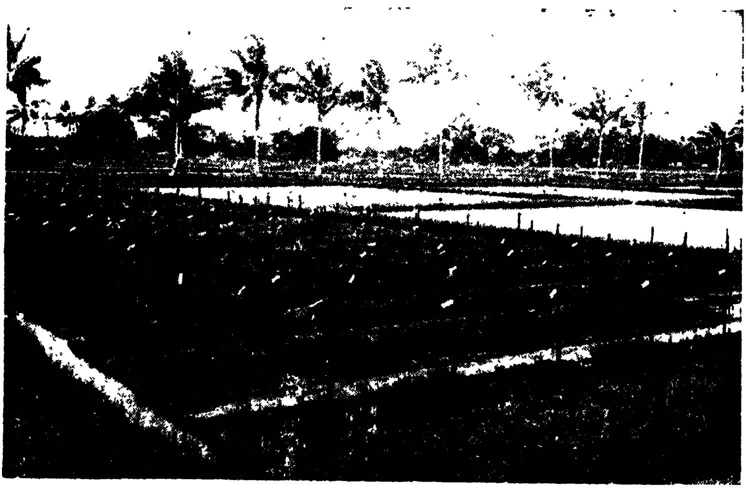
6. Field technique.—The theoretical considerations regarding selection of pure lines are simple, *viz.*, isolation of a desirable homozygous individual and multiplying the same without further contaminations. However, in field practice, great deal of skill and energy are necessary to achieve success. There are two primary difficulties in field trials (1) to account for developmental

variability and to distinguish it from genetic variability, (2) to detect small differences between different cultures. For these two considerations, the

(*Photo from Paddy Specialist.*)

Fig. 112. Produce from single plants is harvested, dried and stored individually without being mixed.

application of statistics is of primary importance and without explanations regarding the various statistical analyses and lay-out of field trials, fuller



(*Photo from Paddy Specialist.*)

Fig. 113. Seeds from single plants are sown individually in small plots. The figure shows nursery beds in the case of rice.

discussion of the problem is not possible here. The salient points in the process of selection of pure lines are mentioned here.

(1) In the first year, a large number of single plants are selected from ryots' fields at the time of harvest. Produce from individual plants are picked separate and numbered. If for any reason, visit to the ryots' fields at harvest time is not possible, bulk samples of seeds from different representative villages are brought to the research station and single plants are selected in the following season. At the time of selecting individual plants important characteristics are noted in respect of each. As yield is subject to great deal of environmental variation it does not form the basis for selection. If a plant happens by chance to be in a fertile patch of the field, then it may be vigorous and bear more fruits on it than another plant in a bad patch. Important economic characteristics not subject to large developmental variations, such as lint length and ginning percentage in cotton are made the basis of selection. If the breeding programme is with any particular object, such as disease resistance, colour of grain etc., selection in the local bulk is made on that basis with the reservation that primary characteristics of the crop are not lost sight of. (2) The single plants are sown in the Research Station and are studied in respect of purity in the characters for which selection was made (Figs. 112, 113 and 114).

(*Photo from Paddy Specialist.*)

Fig. 114. The characters of single plants are recorded to judge their purity.

A large number of cultures are rejected and only a limited number are selected. (3) In the third year the same process is repeated and further rejections are made and few outstanding types are selected. (4) In the fourth, fifth and sixth years the selected plants of the third year are tested in larger plots for their yield using the local bulk or any other standard strain as control for comparison. Such of those as are better than control are finally selected. (5) The fifth step consists in district trials. Very promising selections, if any, are sent for district trials. Outstanding selections from the first year of yield test on the research station, may be sent next year for district trial, thus conducting yield trials on the Research Station and in districts simultaneously.

One or two selections that prove superior to the local at least in three seasons are issued as improved strains. (Fig. 115).

Ryots' Bulk.

The bulk is a mixture of types and can be sorted out. Single plants are selected.

The single plants are sown individually and tested for purity.

The promising ones are later tested for yield in bigger plots using the local type as standard for comparison.

The yield trials are also conducted in the districts in the ryots' fields.

Improved selection is released as a strain from the research station.

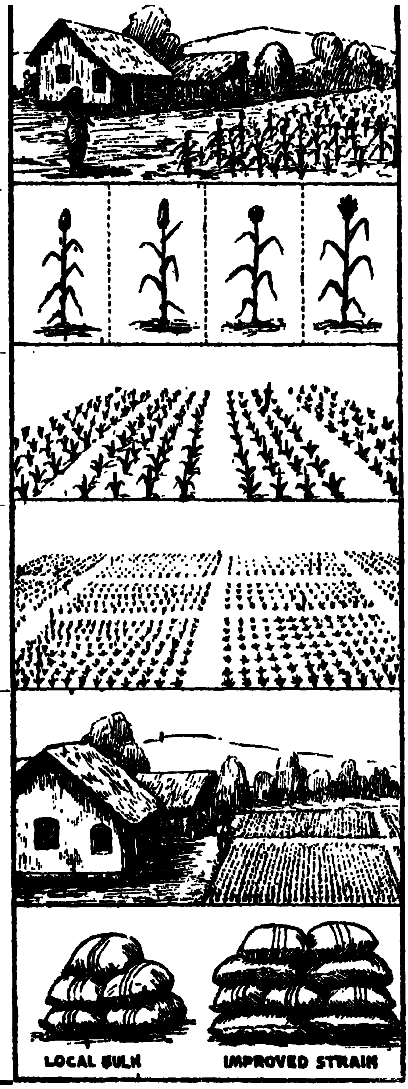


Fig. 115. Diagram to illustrate the various steps involved in pure line selection.

Reference may be made here to the field technique of progeny row test and compact family block which are applied by plant breeders to detect small genetic variability after eliminating fluctuating variability. These increase efficiency of selection and eliminate the personal factor in the selection of plants in the field.

Thus it will be seen that a period of 7–9 years are necessary before an improved strain can be selected in a breeding station.

7. Limitations.—Pure line selection aims at isolation of naturally existing homozygous biotypes. There is no possibility of introducing new charac-

teristics not originally found in the population in which selection is started. Therefore pure line selection reaches its extreme limit when selection has been exhausted in all the local bulks. In Egypt, selection in the local bulks of cotton has been exhausted and this method has been given up as of no further utility to the plant breeders there. The case is different in India where selection on extensive scale has never been carried out in any crop. In Russia, a world wide expedition for collection of all cultivated and allied wild types has been organised, and by this process many useful types not found in Russia have been selected. North-West India, some parts of Himalayas and North-East India are regions where many cultivated forms have originated and as such large scale expeditions to these regions are necessary before primary selection is given up in any crop in India.

Another possibility for improvement of crops is the interchange of improved types by the various Research Stations of various countries.

One danger against which a plant breeder must be guarded is that very stringent pure line selection reduces the scope of the strain to spread to large areas. The utility of such a strain is more and more restricted to small areas. A perfect adaptability to the local conditions with the elimination of chances for future variation, makes the strain unfit for varying conditions which may exist even within one district. A strain which has no adaptability to varying conditions within certain limits, possesses certain drawbacks. (1) To cover a large area under cultivation, such as a Province, a large number of strains is required—say one strain for each taluk. This becomes difficult. (2) the uniformity of the material that is ultimately pooled in a central market is lost. A large number of pure lines, each one adapted to a small tract, has to be mixed up in large markets and consequently the uniformity of market produce and value thereon are lost. Therefore a breeder must not only aim at increasing the yield or quality by pure line selection but also try as far as possible to widen the area of cultivation of the improved type. This is of especial importance in the case of commercial crops. For example, in the case of cotton, the Indian Central Cotton Committee has declared that unless a selected strain spreads to not less than 5,000 acres, it shall not receive recognition as a standard strain.

8. Achievements by pure line selection.—In many crops great advancements were made by selection in natural populations. The following are some of the strains evolved by the Madras Agricultural Department by pure line selection.

Rice (*Oryza sativa*).

ADUTURAI STATION.—

Adt. 1 ... Isolated from red sirumani.

Yields 16% over local bulk. Mainly used as par boiled rice for export.

Yield per acre : 3,023 lbs.
Grain size : 6·4×3·1×2·1 mm.
Glume colour : Dirty in furrows.

Adt. 2 ... Isolated from white sirumani.

Yields 10% over ryots' bulk. Matures earlier than Nellore samba.

Yield per acre : 2,824 lbs.
Grain size : 5·8×2·9×2·0 mm.
Glume colour : straw.

Adt. 3 .. Isolated from Kuruvai. Consumed as parboiled rice. No appreciable increase in yield over ryots' bulk, but is early in duration.
Yield per acre : 3,641 lbs.
Grain size : 7·7×3·0×2·0 mm.

Adt. 4 ... Isolated from Kuruvai. Yields 12% over ryots' bulk.
Yield per acre : 3,784 lbs.
Grain size : 7·9×3·0×2·0 mm.
Glume colour : Dirty in furrows.

Adt. 5 ... Isolated from Nellore Samba. Yields 25% over ryots' bulk.
Yield per acre : 2,790 lbs.
Grain size : 8·1×3·1×2·0 mm.
Glume colour : Dirty in furrows.

Adt. 6 ... Isolated from Red Ottadan. Yields 13% over ryots' bulk.
Yield per acre : 1,960 lbs.
Grain size : 7·7×3·0×2·0 mm.
Glume colour : Dark gold.

Adt. 7 ... Isolated from white Ottadan. Yields 13% over ryots' bulk. Grown as udu mixture with Adt. 3.
Yield per acre : 2,033 lbs.
Grain size : 7·6×3·0×2·0 mm.
Glume colour : straw.

Adt. 9 ... Isolated from Poonkar. Yields 15% over ryots' bulk.
Yield per acre : 4,000 lbs.
Grain size : 8·2×2·8×1·9 mm.
Glume colour : straw.

Adt. 10 ... Isolated from Korangu samba. Yields 9% over ryots' bulk. Exported as parboiled rice.
Yield per acre : 3,888 lbs.
Grain size : 7·2×3·0×2·0 mm.
Glume colour : Dirty in furrows.

Adt. 11 ... Isolated from Nellore Samba. Yields 6% over ryots' bulk.
Yield per acre : 3,438 lbs.
Grain size : 7·4×2·8×1·9 mm.
Glume colour : Dirty in furrows.

Adt. 12 ... Isolated from Chitrakali. Yields 9% over ryots' bulk. Stands irregular water supply.
Yield per acre : 3,527 lbs.
Grain size : 8·7×2·9×2·0 mm.
Glume colour : Straw with slight granular dirty.

Adt. 13 ... Isolated from Sanna Samba. Yields 7% over local bulk. Suitable for upland taluks.
Yield per acre : 3,873 lbs.
Grain size : 8·1×2·6×1·9 mm.
Glume colour: straw.

Adt. 14 ... Isolated from Vellaikar. Yields 9% over ryots' bulk.
Yield per acre : 4,375 lbs.
Grain size : 8·8×2·9×2·0 mm.

Adt. 16 ... Isolated from Konakuruwai. Yields 25% over ryots' bulk.
Yield per acre : 3,669 lbs.
Grain size : 7·7×1·9×1·5 mm.
Glume colour : Light gold.

Adt. 17 ... Isolated from Muthusamba. Yields 10% over local bulk. Coarse bold type of grain.
Yield per acre : 3,700 lbs.
Grain size : 7·8 × 3·4 × 2·2 mm.
Glume colour : Dirty in furrows.

Adt. 18 ... Isolated from Vellaikuruvai. Yields 12% over local bulk.
Yield per acre : 3,600 lbs.
Grain size : 8·1 × 3·0 × 2·0 mm.
Glume colour : straw.

Adt. 19 ... Isolated from Sarapalli. Yields 19% over local bulk.
Yield per acre : 3,780 lbs.
Grain size : 7·9 × 2·9 × 2·0 mm.

Adt. 21 ... Isolated from Vadansamba of Tanjore District. Yields 15·8% over local bulk. Grown in coastal taluks.
Grain size : 8·5 × 3·0 × 2·0 mm.
Glume colour : Dirty in furrows.

COIMBATORE STATION.—

Co. 2 ... Isolated from Poombalai. Suitable for late planting.
Yield per acre : 4,886 lbs.
Grain size : 7·5 × 2·5 × 1·9 mm.
Glume colour : Straw.

Co. 3 ... Isolated from Vellaisamba. Yields 9% over local bulk.
Yield per acre : 4,000 lbs.
Grain size : 8·4 × 2·7 × 2·0 mm.
Glume colour : Straw.

Co. 4 ... Isolated from Anaikomban of Gobichettypalayam. Yields 11% over ryots' bulk. It is a tall growing variety with coarse straw and grain. It is resistant to blast and is good for making puffed rice.
Yield per acre : 3,788 lbs.
Grain size : 8·6 × 2·7 × 2·0 mm.
Glume colour : Straw.

Co. 5 ... Isolated from Chinnasamba. Yields 12% over ryots' bulk. Responds to high manuring.
Yield per acre : 3,500 lbs.
Grain size : 7·9 × 2·6 × 1·9 mm.
Glume colour : Straw.

Co. 6 ... Isolated from Sadaisamba. It is a tall growing and tillering variety. It is suitable for single crop lands where water is available till January.
Yield per acre : 3,890 lbs.
Grain size : 7·7 × 2·8 × 1·9 mm.
Glume colour : Straw.

Co. 7 ... Isolated from Sadaisamba. It tillers profusely.
Yield per acre : 4,150 lbs.
Grain size : 7·9 × 2·7 × 1·9 mm.

Co. 8 ... Isolated from Anaikomban of Tinnevelly. Yields 17% over ryots' bulk.
Grain size : 8·8 × 2·6 × 1·9 mm.
Glume colour : Straw.

Co. 9 ... Isolated from Karsamba-red of Tinnevelly district. Yields 14% over the local bulk. Rice is red.
Yield per acre : 3,000 lbs.
Grain size : 7·4×3·2×2·2 mm.
Glume colour : Dull straw.

Co. 10 ... Isolated from Kar variety of Gobichettypalayam. Yields 17% over the local. Suitable for Kodai and Navarai season and is used for preparing puffed rice.

Co. 11 ... Isolated from Ayansamba of Gobichettypalayam. Yields 13% over ryots' bulk. Lodges in highly manured plot.
Grain size : 8·2×2·6×1·9 mm.
Glume colour : Clean straw.

Co. 12 ... Isolated from Sendhinayagam of Ambasamudram taluk. Yields 13% over ryots' bulk.
Yield per acre : 3,000 lbs.

Co. 13 ... Isolated from Arupathamkodai of Madura. Yields 19% over the ryots' bulk. Can be grown in first crop and late navarai season.
Yield per acre : 3,000 lbs.
Grain size : 7·8×3·1×2·0 mm.
Glume colour : Straw with purple tip.

Co. 17 ... Isolated from Vadansamba of Chingleput District. It yields 25% over the local. It is earlier by 10 days than the local bulk. Its grain is coarse, straw stiff and earhead bunched.
Yield per acre : 2,500 lbs.
Grain size : 8·1×2·8×2·0 mm.
Glume colour : Dull straw.

Co. 18 ... Isolated from Vellaikar of Chingleput District. It yields 12·5% over the local bulk. Rice is white. It is earlier than the local by a week.
Yield per acre : 2,700 lbs.
Grain size : 8·1×2·9×2·0 mm.
Glume colour : Straw.

Co. 19 ... Isolated from Sirumani of Chingleput District. It yields 12% over the local bulk. Comparatively resistant to blast. Rice is white.
Grain size : 7·7×2·8×2·0 mm.
Glume colour : Dirty in furrows.

MARUTERU STATION.—

Mtu. 1 ... Isolated from Akkullu; gives 20% increased yield over the local. Suitable even to saline or submerged areas.
Yield per acre : 2,800—3,700 lbs.
Grain size : 8·0×2·8×2·0 mm.
Glume colour : Dirty in furrows.

Mtu. 2 ... Isolated from Akkullu; gives 16% increased yield over local bulk. Suitable to rich lands where it does not lodge.
Yield per acre : 2,800—3,500 lbs.
Grain size : 7·9×2·7×1·9 mm.
Glume colour : Dirty in furrows.

Mtu. 3 ... Isolated from Potitbasangi; gives 12% increased yield over local bulk. Suitable to rich and early planted areas. Free from lodging.
Yield per acre : 2,000—4,500 lbs.
Grain size : 8·1 × 2·7 × 2·0 mm.
Glume colour : Straw.

Mtu. 4 ... Isolated from Basangi; gives 9% increased yield over local bulk. Suitable to soils of average fertility and indifferent water supply.
Yield per acre : 3,000—4,000 lbs.
Grain size : 8·8 × 2·6 × 2·0 mm.
Glume colour : Straw.

Mtu. 5 ... Isolated from Krishnakatukulu ; gives 12% increased yield over the local.
Yield per acre : 2,800—3,400 lbs.
Grain size : 7·8 × 2·6 × 1·8 mm.
Glume colour ; Straw with purple tip end.

Mtu. 6 ... Isolated from Pottiatragada ; yields 16% over local bulk. Suitable for low lying ill drained areas. Due to short growing habit it is free from lodging.
Yield per acre : 2,800—3,000 lbs.
Grain size : 7·9 × 2·8 × 2·0 mm.

Mtu. 7 ... Isolated from Guttikusuma ; yields 16% over ryots' bulk. It is non-lodging and non-shedding. Can stand indifferent water supply.
Yield per acre : upto 3,500 lbs.
Grain size : 8·6 × 2·7 × 2·0 mm.

Mtu. 8 ... Isolated from Vankisannam ; yields 10% over ryots' bulk. Non-shedding and good setting are its qualities over the local.
Grain size : 8·7 × 2·5 × 1·9 mm.
Glume colour : Medium gold.

Mtu. 9 ... Isolated from Garikasannavarai; yields 18% over local. Suitable for 'Dalwa' season. Can stand early planting and grows well in newly reclaimed coastal parra lands.
Yield per acre : 2,000—3,000 lbs.
Grain size : 8·1 × 2·85 × 2·0 mm.
Glume colour : Straw with purple tip.

Mtu. 10 ... Isolated from Krishnakatukulu. It does not lodge and is adapted to high level rich lands.
Yield per acre : 2,800—3,200 lbs.
Grain size : 7·5 × 2·3 × 1·7 mm.
Glume colour : Straw with purple tip.

Mtu. 11 ... Isolated from Konamani ; yields 30% over the local. Can grow under deep water conditions.
Yield per acre : 3,000 lbs.
Grain size : 8·1 × 3·0 × 2·0 mm.
Glume colour : Dull straw.

Mtu. 12 ... Isolated from Peda Atragada. Suitable for low-lying areas.
Yield per acre : 3,150 lbs.
Grain size : 8·2 × 2·8 × 2·1 mm.
Glume colour : Dark dirty in furrows.

Mtu. 13 ... Isolated from Delhi bhogam ; suitable to well-drained soil of higher delta.
Grain size : 8·2 × 2·2 × 1·7 mm.
Glume colour : Light gold.

Mtu. 14 ... Isolated from Atragada ; yields 9% over Mtu. 6. It is characterised by thick straw and vigorous growth. Does not lodge. Suitable for illdrained soils at tail end of canals.
Grain size : 7·9 × 2·7 × 2·0 mm.
Glume colour : Dirty in furrows.

PATTAMBI STATION.—

Ptb. 1 ... Isolated from Aryan variety of South Malabar ; yields 15% over ryots' bulk. Its rice is red.
Yield per acre : 3,000 lbs.
Grain size : 8·2 × 2·9 × 2·0 mm.
Glume colour : Dirty in furrows .

Ptb. 2 ... Isolated from Ponnaryan ; suitable for single and double crop lands. Yields 15% over ryots' bulk. Its rice is red.
Yield per acre : 2,500 lbs.

Ptb. 3 ... Isolated from 'Eravapandy' ; yields 8% over local bulk. Recommended for areas with water scarcity by January end. Its rice is red.
Yield per acre : 1,800 lbs.
Grain size : 8·6 × 2·8 × 2·0 mm.
Glume colour : Dirty in furrows.

Ptb. 4 ... Isolated from Vellari ; yields 22% over local bulk. Heaviest yielder of second crop varieties provided water supply is assured upto end of January.
Yield per acre : 2,200 lbs.
Grain size : 8·1 × 3·1 × 2·1 mm.
Grain colour : Dull straw.

Ptb. 5 ... Isolated from Velutharikayama ; heaviest yielder of first crop varieties. It yields 15% over the local bulk.
Yield per acre : 2,700 lbs.
Grain size : 8·4 × 2·9 × 2·0 mm.
Glume colour : Dull straw with granular dirty patches.

Ptb. 6 ... Isolated from "Athikraya". It yields 18% over the local bulk.
Yield per acre : 2,000 lbs.
Grain size : 8·0 × 3·1 × 2·0 mm.
Glume colour : Dark dirty in furrows.

Ptb. 7 ... Isolated from Parambuvattan. It yields 13% over ryots' bulk. It tolerates irregular water supply and salinity in soil. Its rice is red.
Yield per acre : 2,350 lbs.
Grain size : 8·0 × 2·8 × 2·0 mm.
Glume colour : ripening black.

Ptb. 8 ... Isolated from Thavalakkannan ; it yields 17% over local bulk, and is earlier by a week. Its rice is red.
Yield per acre : 2,500 lbs.
Grain size : 7·3 × 2·9 × 2·0 mm.
Glume colour : Dull straw with purple tip.

Ptb. 9 — Isolated from Thavalakkannan. It yields 13% over the local. It is erect, tall and non-shedding. Its rice is white.
Yield per acre : 2,900 lbs.
Grain size : $7 \cdot 4 \times 2 \cdot 9 \times 2 \cdot 0$ mm.
Glume colour : Dull straw with purple tip.

Ptb. 10 — Isolated from thekkancheera suitable for third crop season maturing in 100 days. Its rice is red. Can stand irregular water supply.
Yield per acre : 2,100 lbs.
Grain size : $8 \cdot 1 \times 2 \cdot 9 \times 2 \cdot 0$ mm.
Glume colour : Dirty in furrows.

Sorghum. sp.

COIMBATORE STATION.—

A.S. 29 ... Isolated from Periamanjal. It yields more grain and straw than the ryots' bulk. It is popular as a fodder type.

A.S. 389 ... Isolated from Sencholam. It yields better than the local bulk of Trichinopoly and Salem districts.

A.S. 809 ... Isolated from Chinnamanjal cholam : It is an irrigated yellow grained variety.

A.S. 1543 ... Isolated from a white grained irrigated Sorghum. Duration 110 days.

A.S. 1575 ... Isolated from Vellaicholam. Duration 100 days.

A.S. 2095 ... Another selection from Vellaicholam. Duration 95 days. It has compact ears with slightly red tinged grains.

A.S. 3355 ... Good as a fodder variety. It has juicy stalk.

A.S. 3313 ... Isolated from Thalaivirichan cholam.

HAGARI STATION.—

T. 1 ... Selection from Tellajonna of Hagari.

T. 12 ... Selection from Tellajonna of Raichur. Loose earhead.

Pearl Millet (Cumbu) (*Pennisetum typhoides*).

COIMBATORE STATION.—

P.T. 2229 — Selection from Kottapuli cumbu of Salem District. Tillering poor, setting compact and grain size medium. Duration 80—90 days.

P.T. 248 — Selection from Kattukambu of Coimbatore. Tillering fair, setting medium compact and grain medium to small size. Duration 85—95 days.

KOILPATTI STATION.—

K.C. 292 ... Kullan cumbu ; 75 days in duration.

K.C. 105 ... From "Punjab cumbu" 95 days in duration. Grain not so palatable as K.C. 8.

K.C. 8 ... Kattu kambu of Koilpatti, 95 days in duration. A popular strain.

Ragi (*Eleusine coracana*).

COIMBATORE STATION.-

Co. 1 ... Selected from Gidda aryan of Salem. 4 months in duration. It may be raised as rainfed crop when the rainfall is over 40". In Vizagapatam and Chittoor districts it is popular as a dry crop.

Co. 2	Selected from Mutti ragi of Udamalpet, 110 days in duration under irrigation. Suitable for Chingleput, Chittoor, North Arcot, Tanjore, Salem, Coimbatore and Madura districts.
Co. 4	Selection from local bulk of Palladam. 130—140 days in duration. Under irrigation, yields 2,250 lbs. per acre. Suitable for Ramnad and Tinnevelly districts.

ANAKAPALLE STATION.-

AKP. 1	Selection from Burada Chodi. 70 days in duration. Yields 2,500 lbs. per acre. Suitable for wet lands in Vizagapatam district.
AKP. 2	Similar as AKP. 1. Duration 85 days.
AKP. 3	Selection from Pyruchodi. 100 days in duration. Yields 1,200 lbs. per acre. Suitable for Pyru season in Vizagapatam district.
AKP. 4, *AKP.* 5	Selections from Pyruchodi and similar to AKP. 3.
AKP. 6, *AKP.* 7	Selections from Peddachodi. Suitable for Pyru season in Vizagapatam district.
*BBL.*5	Isolated from Buradachodi of Bobbili. Big and attractive earheads. Duration 90 days. Punasa crop.
V. 33	Isolated from Vesangichodi of Vizianagaram. 100 days in duration. Pyru crop.
No. 525	Isolated from Buradachodi of Vizianagaram. 85—90 days in duration. Profuse tillering; earhead small. Punasa and Pyru crop.

Korra (*Setaria italica*).

GUNTUR STATION.—

G.K. 6 ...	Isolated from Punasakorra of Palnad. 90 days in duration.

NANDYAL STATION.—

N.K. 132 ...	Isolated from Sena Korra of Nandyal; yields 10—15% more than the local. 90 days in duration.
N.K. 140 ...	Isolated from Sena Korra of Nandyal; yields 10—15% more than the local.

HAGARI STATION.—

H.K. 23 ...	Isolated from Asunda of Bellary; yields 10—15% more than the local. Shorter in duration by a week. Comes up even in years of poor rainfall in soils varying from sandy to black soils.
H.K. 68 ...	Isolated from Paramadevanahalli of Bellary. Better suited to deep black soils than H.K. 23.

Varagu (*Paspalum scrobiculatum*).

COIMBATORE STATION.—

P.S. 1	Isolated from Kalipalayam local bulk. It is rainfed. Tillering good. Leaves with purple splashed margin. Duration 150 days. Grain brown in colour.

Cotton (*Gossypium sp.*).

Co. 2	Isolated from Cambodia bulk; staple ⅞″—1″; ginning percentage 35; spinning 35's. It yields 250 lbs. lint under irrigation and 100 lbs. lint under dry conditions. It is a hardy cosmopolitan type.

HAGARI STATION.—

H. 1 It is a pure line selected from the 'westerns' *G. herbaceum var. frutescens*;. staple ⅞"—15/16" Ginning percentage 29. Spinning 24's to 36's. Early in maturity and medium in staple. It yields 72 lbs. lint.

NANDYAL STATION.—

N. 14 ... It is a pure line from white linted northerns—*G. arboreum var. neglectum forma, indica*. Staple 1". Ginning percentage 23. Spinning 40's to 44's. It is a poor ginner. It is late, strong and fine linted.

KOILPATTI STATION.—

K. 1 ... Is a re-selection from C-7. *G. arboreum var. neglectum forma indica*. Staple ⅞"—15/16". Ginning percentage 32. Spinning 24's to 30's. It is an early type. Yields 105 lbs. lint.

Chapter 17

CLONAL SELECTION

CLONES — CLONAL VARIATION — BUD MUTATION — IMPROVEMENT IN CLONES—SUGARCANE SELECTION TECHNIQUE—BANANA BREEDING

1. Clones.—In cultivating the different crops, it is not always expedient to propagate them by sowing the seed. In some cases, the crops are raised by adopting vegetative methods of propagation. This method is adopted either due to lack of seed production in the plant as in bananas, or the cultural practices and climatic conditions at planting time may give better crop if this method of propagation is adopted, as in the case of onion. In some cases vegetative propagation is the method to ensure purity of the race as in the case of some fruit trees like mangoes, oranges, apples, etc.

The morphological part used in vegetative propagation may be different in different plants as shown below :—

Cuttings from stem	Sugarcane. Betel vine. Sweet potato. Ornamental plants like crotons, etc. Avenue trees such as Portia tree. Hedge plants like *Glyricidia maculata*.
Tubers, corms and bulbs ...	Potato, yam, colocasia, onion, garlic, etc.
Suckers	Bananas, aloe, agave, pine-apple.
Division of crown	Herbaceous plants such as fodder grasses.
Grafts and buds	Fruit trees such as mangoes, citrus, apple, pear, etc.
Layering	Flower plants like rose, jasmine, etc.

There are many other methods of vegetative propagation such as formation of root suckers, and bulbils.

The plant may resort to asexual propagation if it is a hybrid with meiotic irregularities or other genetic causes which enforce sterility. Some of the important crop plants such as sugarcane, bananas, etc., are thus vegetatively propagated due to poor or absence of seed formation. A variety that is propagated vegetatively from a single original stock is termed a *clone*.

Other conditions that are genetically equivalent to clones may arise in plants. In some fruit trees such as mangoes and citrus, *polyembryony* is frequent. In these cases, only one embryo or none at all, is the resultant of true fertilisation. The other embryos are formed from vegetative cells of the ovule. They may arise from nucellus or integuments. These enbryos are genetically true to the mother plants. Development of unreduced egg without fertilisation, termed *parthenogenesis*, may also take place. Such progenies are also identical with the mother plants. In all the cases of vegetative reproduction the progenies breed true to the mother plant from which they arise

2. **Clonal variation.**—In mitotic cell division, there is no mechanism that permits of variation of daughter cells from the mother cell. It may be recalled that in meiosis, the homologous chromosomes pair, exchange genetic material between themselves and the chromosome number in daughter cells is reduced to half. By the union of gametes sometimes from different parents, variation arises in the sexually reproduced progenies. In contrast to the sexual reproduction, when a "cutting" or its equivalent is used for propagation, the cells divide by mitosis and the two daughter cells are identical with the mother-cell. Therefore, the group of plants that is derived by vegetative propagation from a single plant breeds pure clonally. As in the case of pure lines, groups of plants derived from genetically different parental stocks may show variation. Numerous varieties, especially in the case of fruit trees such as mangoes and citrus, have been established and multiplied by vegetative propagation from a single selected plant. Therefore, descendants of a single variety do not show variations within themselves.

Most of the variations within the clones in respect of quantitative characters are due to the effects of environment. By the application of statistical interpretation to yield data from orchards, it is found that a large part of the variation is due to seasonal variations, soil heterogeneity and other developmental causes. In the case of apple, the following data are reported.

Seasonal variation	62%
Soil heterogeneity	18%
Stock heterogeneity, genetic bud variations and unknown causes	15%

(*From Babcock & Clausen*)

It has further been noted in the case of orchard trees that selection of high yielding scions for propagation has no permanent effect due to the fact that the choice of stock has great influence over the future growth and yield. Therefore improvement in orchard trees must first be sought in the choice of proper stock and other orchard cultural practices. Selection of high yielding scions must be based on genetic variability which is made difficult due to the masking of the same by developmental variations. Variations between clones must either have their origin from the genetic difference between the first parental plants from which they have been vegetatively propagated or the variations must have arisen by bud mutation.

3. **Bud mutation.**—Though mutation is most frequent at maturation divisions, they may also arise in somatic cells. If mutation occurs in cells from which buds are developed, the latter are genetically different from the rest of the plant. These are termed "*bud mutations*" or "*sports.*" The frequency of such mutations is very low to be of any economic importance. The frequency of such bud mutations is different in different species. The bud mutation may arise by (1) gene mutation, (2) chromosomal variation, (3) chimera.

Bud variations have been noted in sugarcane. This was first noted by Louzier in Mauritius in 1869. Other instances of sporting are Ribbon canes

of Australia, Truna canes of Mauritius and Tip canes of Hawaii. P.O.J. canes also have been found to throw bud variations. Barber (1906) noted

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Fig. 116. Bud mutations from sugarcane Co. 213. *Note* the Variations.

bud sports in the sugarcanes at Samalkota. Striped-Mauritius oftener sported into green canes and less often into red types. The bud sports not only varied in the colours on rind but also in some of the agricultural characters. Co. 213 has been found to throw bud variations. (Fig. 116). Bud sports are frequent in ornamental plants and many new garden varieties have been established by selection of such sports. Economic types from bud sports in the case of field crops are rare. Though bud sports have been noted in crops like potato, they have not been found to be of economic type. Superior varieties in citrus have been evolved by selecting bud mutants. It is reported that in 18 years prior to 1937, about 10 million buds of varieties which originated by bud mutation have been sold in California alone. Robertson Navel orange and Dawn grape fruit are some notable examples of new varieties arising by bud mutation.

4. Improvement in clones.—It has been pointed out that variations in yield in the case of clones are largely due to environment. Detailed studies have been carried out in the case of potatoes and it was found that yields from different stocks were largely influenced by (i) presence of diseases in seed stock, (ii) agronomic conditions under which the seed stock has been raised, (iii) soil conditions under which the crop is raised, (iv) genetic variability. Of these four, the last mentioned one is always small enough as compared to others and also is not easy to detect. Since bud variations are rare and when present are not always agronomically important, variations in clones are to be sought by raising progenies through seeds. The plants of a clonal population may be all alike but they all may not be homozygous. Even heterozygous plants when asexually propagated, yield identical progenies. *Therefore when seeds are sown, large variations among seedlings are noted.*

Fig. 116-A. Bud mutations in Co. 213. Note the variations in cane.

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It is for this reason that improved types of fruit trees such as mangoes, citrus, etc., are not raised by sowing seeds from improved stock but are propagated by vegetative means such as grafting and budding. Among the commercial varieties of mangoes, Chinnasuvarnarekha and Mundappa are examples of varieties from seedlings. Naturally cross-fertilised seeds gave rise to these varieties and the original trees are reported to be still alive. When the chance seedling was discovered, further propagation was by grafts.

In the case of sugarcane, fertility of the seed was first noted in 1886 by Soltwedel in Java and Harrison and Bovell in Barbados. Most of the seedlings did not prove useful but some were disease resistant. Soon, the seedling canes ousted the local canes. Further improvements were effected by hybridising the noble canes (*Saccharum officinarum*) with wild canes, *Sorghum*, and bamboo. The hybrid seeds are sown and the desirable seedlings are selected and further vegetatively propagated.

In the case of potatoes too, selection is practised by raising seedlings through seeds. Varieties are hybridised and then sown. Selected progenies are multiplied vegetatively and thus there is no need to study segregation in the progenies or purify them because vegetative propagation ensures breeding true to parental type and there is no fear of deterioration of the selected type.

In the case of orchard plants, choice of disease free plants and elimination of poor yielders are the first steps for improving yield. Individual tree records are to be maintained and poor yielders are to be eliminated. Especially, chimeras and bud sports are to be removed. Very often, the buds of stocks may also grow with the scion and thus poor yields and inferior fruits are the results. Desirable root stocks should be selected for grafting and budding. Cultural practices in the orchard are also found to largely influence the yield.

5. Sugarcane selection technique.—As an example for clone, the technique for selection of improved types in sugarcane as adopted at the Imperial Sugarcane Station at Coimbatore is detailed here.

It was pointed out that the germinability of the sugarcane seeds was first discovered in 1886 and this marks the beginning of sugarcane breeding. Previously the sugarcane inflorescence was described as completely sterile. This misapprehension is due to the fact that the seeds lose their viability within a few weeks after their ripening and also many florets in fertile varieties are empty.

Sugarcane flowers under short day conditions. In the northern hemisphere it arrows from October to December and in the southern hemisphere from March to June. There are varietal differences in flowering habit. The arrowing is also largely influenced by carbohydrate-nitrogen relationship in that excess of nitrogen lowers the percentage of arrowing and deficiency in that element increases arrowing. Many varieties of sugarcane are male sterile. Varieties with abundance of pollen may be self-sterile, partially self-sterile or highly fertile.

On selfing the arrows, few seeds set in the self-fertile varieties. In these cases, the phenomena of production of defectives as in naturally cross-fertilised crops like maize are noticeable. The arrows may either be selfed or crossed and the resultant seeds are sown for raising seedlings. The technique of crossing is described in Chapter XVIII.

The work at Coimbatore is mainly for providing suitable types for the sub-tropical regions of India. Quickest results for India were obtainable by sowing the seeds secured by cross-pollination. Nearly a lakh or a lakh and half seedlings are raised each year at this station and they comprise of complicated cross-pollinations. Wild *Saccharums* have played important role in the breeding of improved sugarcanes. The arrows which (Fig. 121) have been cross-pollinated are collected and stored by loosely packing them in tissue papers. These are dried in the sun for two days. The fluff is stored in well ventilated place. The fluff is sown in earthenware pans and carefully watered. The seeds germinate in three days. If the seedlings are too much crowded they are thinned out. After one month, the seedlings are transplanted into first ground nursery (Fig. 117). Raised beds two feet broad

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Fig. 117. First ground nursery.

and four inches tall are formed at two feet interval in the nursery. No selection is made when planting from pots into the first ground nursery. The plants are allowed to grow in the first ground nursery for about two months when they are about 9" to 12" tall. They are then carefully planted into second ground nursery. Here too, the plants are not selected. From second nursery the plants go to plots for testing, and the planting is done by taking setts from the seedlings. Botanical, chemical and agricultural characters are studied at this stage. Selection of seedlings is made based on various characters such as vigour, habit, and tillering. Parents, grand parents and standard canes are also planted in the margins of test plots for comparison. The

Fig. 116-B. Variations in clones. Note the uniformity in the progenies that arise by vegetative propagation (left) and the variations that arise by sexual propagation i.e. sowing of fluff (right).

(Unpublished drawing by courtesy of Sugarcane Expert, Coimbatore.)

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performance of seedlings particularly in regard to critical period of the tract, is noted. Selection of canes during bad seasons has been more useful than the selections made in good years. The new canes are periodically compared with the standard canes. Seedlings showing defect in any of the important characteristics are rejected. This enables to restrict the work to few useful new seedlings. The selected seedling canes are later sent to several district research stations for further trial. Since sugarcane is propagated by setts, even complex hybrids can be raised year after year without any chance for heterozygous characters to segregate. This is in contrast to the breeding work in sexually propagated plants. Coimbatore seedling canes have spread to many other countries also (Fig. 139).

6. Banana breeding.—Valuable work has been done in this crop in Trinidad. The most important commercial variety Gros Michel is susceptible to Panama disease. There are several varieties which are immune to Panama disease but they are not commercially desirable. Re-combining of these desirable characters by breeding is beset with some difficulties. (1) the commercial types are sterile and produce no seeds. (2) they must be induced to set seed for purposes of breeding work. (3) the seed bearing character must be eliminated from the selected types.

In fertile varieties pollen development is regular and a few seeds are formed. Crosses between fertile varieties result in sterility of the hybrid but pollen fertility increases in the back crosses. At Trinidad, the breeding work was mainly on Gros Michel ; *Musa malaccensis* which is immune to Panama disease was selected as the male parent. By cross-pollination, 49 perfect seeds were secured of which 17 germinated and 5 seedlings only survived. Of the hybrid seedlings one seedling produced fair sized fruit of good flavour. This was resistant to Panama disease and was named I.C.I. It has certain commercial disadvantages and when propagated by suckers, it occasionally sets seeds. Further attempts to improve I.C.I. were made by back crossing to the parents. Gros Michel and I.C.I. proved to be cross sterile and the latter showed double complement of Gros Michel chromosomes and achievement of practical results was found uncertain by back crossing.

Introduction of varieties from various other countries was then tried. Twenty seeded-types and forty edible cultivated types were selected for further work. In introducing these types great care had to be taken to prevent introduction of new diseases at the central station. The suckers were first under quarantine in Kew and then at Trinidad before they were planted in the fields. The breeding work was carried out on the following lines :

(1) breeding from Gros Michel.
(2) breeding from other edible varieties.
(3) breeding from seeded types.

The inflorescences of male and female parents are covered with calico bags and the pollen of the male parent is dusted on to the stigma of the female when the flowers open. The bunches from these inflorescences are collected separately and seeds are removed from the fruits. These seeds are sown in

pots and later the seedlings are planted in the nursery. Suckers from the stools of nursery are transplanted in the field. Since banana varieties are highly sterile, seed setting is poor and also many of the seeds do not germinate, and some of the seedlings exhibit abnormal growth or die due to poor growth and other causes. Thus in one year, out of 1,000 inflorescences pollinated, 474 seeds were produced of which 42 seeds only germinated. Gros Michel is crossed with edible varieties producing abundant pollen and also with fully fertile varieties. Attempt is made to secure F_2 generation from I.C.I. Back crossing the latter to the male parent did not yield any useful result.

The basic chromosome number of the banana is 11 and the common edible types are triploids. Therefore many of the varieties are sterile due to irregularities in pollen development.

Chapter 18

HYBRIDISATION TECHNIQUE

EARLY WORK—TECHNIQUE OF HYBRIDISATION—ANTHESIS—EMASCULATION— ARTIFICIAL POLLINATION—NATURAL CROSSING—CULTURE OF PARENTS

1. **Early work.**—Hybridisation in the case of animals is known for over 2,000 years. In the case of plants too, many of the Chinese varieties of rice mentioned in ancient literature have been evolved by hybridisation. Though in 700 B.C. artificial pollination in date palms was known in Assyria and Egypt, the presence of sex in plants was not demonstrated until the 17th century. Camerarius (1694) drew attention to sex in plants like castor, mulberry and maize. Kolreuter (1760) carried out the first hybridisation experiments in tobacco and he was followed by Knight, Goss, Gartner and others. However, the principles underlying inheritance of characters were not understood until the re-discovery of Mendel's work in 1900. The early work has been reviewed in Chapter I.

2. **Technique of hybridisation.**—The main object of hybridisation work lies in the fact that *the breeder wishes to artificially create a variable population for the selection of types with desired combination of characters.* Valuable characteristics may be found scattered in different races, varieties or species and by repeated hybridisation, a single type combining all the good characteristics is sought to be evolved.

If the characters are governed by large number of genetic factors, the recombined homozygous types will form a low proportion in the total F_2 population. It will be shown later that there are other genetic phenomena which restrict the recombinations and reduce this proportion still further.

In nature, plants may be self or cross-fertilised according to the floral devices. The plants may bear hermaphrodite flowers or unisexual flowers and in the latter may be monoecious or dioecious. *All dioecious plants are compulsorily cross pollinated.* The *technique of hybridisation mainly consists of processes to ensure the pollen and stigma of known plants being brought together.* For this purpose, the time of shedding and viability period of pollen grains and the emergence and receptivity of stigma are to be first studied. The stamens are removed carefully with the aid of forceps or scissors and this is termed *emasculation.* The flowers are protected from contamination by foreign pollen brought about by natural pollinating agencies. At the time when the stigma is receptive, mature pollen from the desired male parent is artificially dusted on to the stigma and the latter is continued to be protected till the stigma is no more receptive or has lost its function.

The crossed flowers are suitably labelled and the following details are noted :—

(1) Date of crossing.
(2) Details of ♂ parent.
(3) Details of ♀ parent.
(4) Date of picking the crossed fruit.
(5) Remarks.

When a large number of flowers are crossed, the flowers are serially numbered by tying labels to their stalks. The labels should be as light as possible because heavy labels increase shedding of flowers. The details of crosses are noted down in a field record book against the respective serial numbers.

The following are some of the field appliances which are required for emasculation and crossing in the case of ordinary field crops :

(1) Fine-pointed, straight or curved scissors.
(2) Hand lens.
(3) Mounted needles.
(4) Paper covers or cloth bags as the case may be for protecting the ♂ parent, emasculated and crossed flowers.
(5) Small camel hair brush.
(6) Tubes or dishes for collecting pollen grains.
(7) Field labels of suitable size for marking crossed flowers.
(8) Stakes and field labels for marking the selected parents if they are not already marked individually.
(9) Field records.

In the case of crops where special devices are known for emasculation and dusting, all the necessary apparatus and devices are to be taken.

Minuteness of floral parts, injury following emasculation, physiological conditions favouring shedding of crossed flowers, sterility due to physiological or genetic causes are some of the problems faced by a breeder.

3. Anthesis.—A study of flower opening and pollination is termed *Anthesis.* When the stamens are mature, the anther sacs burst open and shed the pollen grains. When the pistil is mature, the stigma becomes receptive and invariably *during the period of receptivity it is fresh and coated with sugary syrup.* The flower bud opens, and the sepal and petal which show various aestivation in the bud fall apart exposing the essential organs. In the case of grasses, lemma and palea play this part. The dusting of stigma with pollen grains takes place at different stages of flower opening depending upon the floral mechanisms in the plant and the relative timing of the various processes.

Before any crossing programme is undertaken, a thorough knowledge of the floral parts and anthesis in the crop concerned is essential to enable the breeder to emasculate and cross the flowers at the proper time. The actual

time at which the various processes take place varies with the environmental conditions.

As has been pointed out already, the crops may be naturally self or cross-pollinated and the floral devices may be adapted for one or the other of the processes.

Self-fertilised plants are hermaphrodite and self-pollination may be effected by any of the following devices :

(*a*) *Cleistogamy* : the flowers do not open at all and self-pollination is the rule.

(*b*) Pollen grains are shed before the flower opens.

(*c*) Protandry : Where the anther sacs burst open first and the stigma elongates through the staminal column full of pollen dust and in the process gets pollinated. The emergence of stigma takes place shortly after the shedding of pollen grains and before the latter have lost viability.

(*d*) The stigma and stamen are hidden by accessory organs even after flower opening. Self-pollination takes place.

(*e*) Insects are allowed to enter the flower but they cannot emerge out until self-pollination is effected and the flowers fade out.

In the case of cross-pollinated crops the floral devices may be any of the following :

I. *Hermaphrodite flowers* :—(*a*) The plants may bear hermaphrodite flowers, but cross-pollination results on account of floral devices, such as mechanical obstructions for self-pollination (herkogamy) or different periods of maturity of the pollen and stigma (dichogamy).

(*b*) Self-pollination may be prevented due to self-sterility and self-incompatibility as it happens in apple, pear, potato, tobacco, etc.

(*c*) Male sterility controlled by genetic factors may cause development of defective pollen only, while the stigma is normal and functional.

II. Monoecious plants with devices for cross-pollination such as in the case of maize and coconut.

III. Dioecious plants where cross-pollination is the rule *e.g.*, date palms or palmyra palms.

After studying the floral parts, it is necessary to study the time of the day when the following phenomena take place so that the proper time for emasculation and dusting may be determined.

(i) The time when the accessory floral parts begin to fall apart and open out, the total time occupied in completing the process, the duration for which they remain open, the time when they

begin to close, whether the process is repeated in the same flower on succeeding days.

(ii) The time when the stamens begin to emerge out or when the anther sacs burst open : whether this takes place before, during or after the accessory parts have opened out : whether the stigma is receptive at the period when pollen grains are shed : whether there is mechanical obstruction between the two sexes to prevent self-pollination.

(iii) The time when the stigma protrudes out : whether at the time the pollen grains are ready to dust it ; whether there are devices to aid or prevent self or cross-pollination, such as visit by bees, butterflies, etc.

(iv) The period for which the pollen grains are viable and the stigma is receptive.

(v) If the flowers open and close repeatedly, the proportion of self or cross-pollination that takes place at different periods : the percentage of setting if there is dimorphism ; the percentage of setting in each type.

(vi) Seasonal and geographical variations, if any, in the same variety.

(vii) The effect of climatic and other environmental factors on the timing of the various processes.

(viii) Varietal differences if any.

Some of the observations made in field crops are briefly summarised here.

1. **Rice.** (*Oryza sativa*).—In America, Jones concludes that cultivated rice varieties may bloom between 6 a.m. and 4 p.m. The actual time of blooming depended upon the atmospheric conditions and the variety. In California, most of the varieties bloomed between 12 noon and 2 p.m. and more flowers bloomed between 2 and 4 p.m. than between 10 a.m. and 12 noon. Most of the flowers on the panicle finished flowering in 6–7 days and the maximum blooming was on 2nd or 3rd day. Lande and Stasel in Texas reported correlation between rates of blooming and vegetative growth. Adair from America reports, that temperature has marked effect on blooming and humidity has much less effect. In tropical regions, flowering is much earlier.

Minimum temperatures for blooming range from 59°F. in North Japan to 77°F in different parts of India. Ramiah from Madras specifies the maximum temperature at 82—84°F, Kobayasi from Japan, fixes it at 86° ± 3.6°F and Akemine from the same place, specifies 95°—104°F. as optimum.

Noguti, specifies both temperature and humidity as affecting anthesis. According to him, flowering starts at 8 a.m. when the temperature is 80°—83° and it ceases at 122°F. 70 —80 per cent. moisture is the optimum and below 65 per cent. flowering is slow and it may continue upto 50 per cent. humidity. In New South Wales, it does not commence below 72°F and 62 per cent. humidity and here the flowering curve is reported to follow the humidity curve.

The flowering is from above downwards in the panicle but in the branches it is not strictly so. The tip one is the first and the basal one second to flower in any branch of the panicle.

Sarangapani (Bengal) observed, that the time of blooming varied with the time of the year. Early varieties flowering in July—August bloom at 7 a.m. while transplanted paddy in October blooms at 9 a.m. In cloudy days, blooming is delayed.

Thompstone (Upper Burma) observed, blooming to be between 7 and 10 a.m. dewy mornings being more favourable. Torrep (Philippines) records 9—11.30 a.m. as the time of blooming. The bearded varieties bloom 3 days after emergence of panicle from sheath while non-bearded varieties may bloom

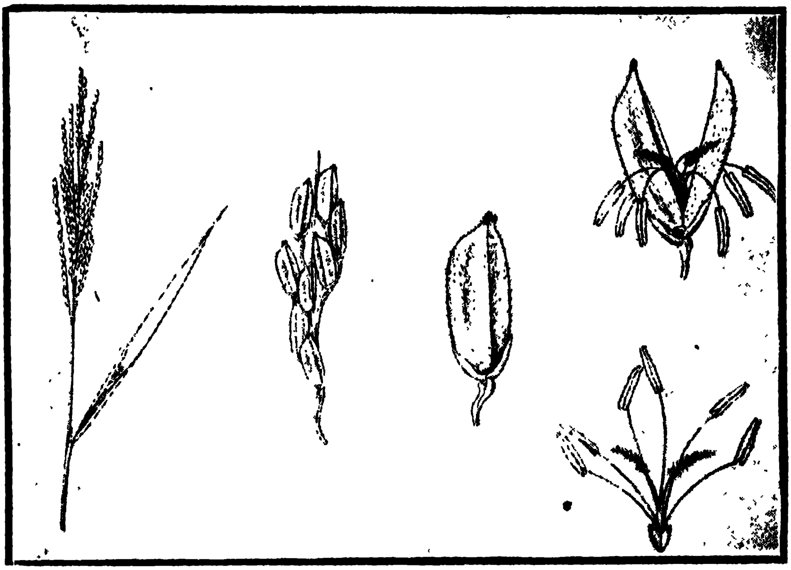

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Fig. 118. Blooming in Rice.

the next day. Vander Stock (Java) reports, that blooming is never before 6 a.m. or after 3.30 p.m. and that the maximum blooming is between 10 a.m. and 12 noon.

The spikelets require $1\frac{1}{2}$ to 3 minutes to open and the closing range (Rao at Tanjore) is from 27 to 54 minutes. According to the same author, the temperature range for early varieties is 79°–84°F. whereas the late ones commence flowering between 85° and 90°F. The entire period from opening to closing is 55 to 60 minutes. Dehiscence and pollination are simultaneous with flower opening.

The panicle emergence is 4-5 days after the flag is out.

Oryza latifolia blooms between 5–7 a.m. when the temperature is 72°F. *O. longistaminata* blooms between 12 noon and 2 p.m. at 90°F. which tem-

perature is 4 to 5 degrees above that for cultivated types. The temperature in the case of 4 cultivated types, flowering on different dates is noted in Table 72:

TABLE 72.

Date.	T. 415.		E. B. 183.		T. 426.		P. S. 42.	
	Blooming time.	Temperature.	Blooming time.	Temperature.	Blooming time.	Temperature.	Blooming time.	Temperature.
26—12—1924 ...	10-45 A.M.	78°	10-30 A.M.	77°	10-45 A.M.	78°	11-04 A.M.	80°
27—12—1924 ...	11-40 ,,	78°	11-30 ,,	78°	11-00 ,,	77°	11-40 ,,	78°
28—12—1924 ...	11-10 ,,	78°	11-20 ,,	78°	11-20 ,,	78°	11-10 ,,	78°
...	..	...	12-20 P.M.	80°	12-20 P.M.	80°	...	...
29—12—1924 ...	12-30 P.M.	80°	11-50 A.M.	78°	12-15 ,,	79°	...	...
30—12—1924 ...	12-20 ,,	80°	12-20 P.M.	80°	12-20 ,,	80°	12-20 P.M.	80°
31—12—1924 ...	11-40 A.M.	79°	11-40 A.M.	79°	11-40 A.M.	79°	11-20 A.M.	78°

In this crop, three types of pollination are possible: (*a*) anthers burst open and pollination has taken place when blooming. This generally happens at high temperature and low humidity. (*b*) The usual process is that the anthers burst as they emerge and pollinate the stigma and (*c*) under certain temperature and humidity the anthers may emerge without bursting and such flowers are cross-pollinated. The emergence of anthers without bursting is more marked in long grained types.

Under New South Wales conditions, the time taken for glumes to open out making 30° angle is between 60 and 180 seconds but it may go upto 7 minutes. The flowers remain open from 13 to 75 minutes after which they close.

2. **Sorghum.**—The reproductive phase is indicated by swollen tip. When the 'flag' has emerged the 'boot' also slowly comes out. It takes about 9 days to emerge. In longer duration varieties it may take longer time.

The panicle takes 5 days to emerge clear from the boot. In about another 5 days the panicle is pushed aloft by its stalk. In the compact headed Deccan varieties, the panicle may get clear of the boot by a twist of the stalk. The panicle consists of a central stalk and a number of branched laterals which bear the spikelets. The spikelets occur in twos, one being sessile and the other pedicelled ; the former is bisexual and the latter unisexual and male. In the panicle, the order of flowering is from top downwards until it is upto halfway down when a second wave of anthesis of male flowers starts from the top and overlaps the first flush.

There may be 2,000 to 4,000 spikelets in an ear-head and it takes 8 days for blooming to complete and the maximum number of flowers open between 3rd and 6th days.

(*Photo from Paddy Specialist.*)
Fig. 119. Blooming in rice.

The flowers open in the night. The exact time of opening may vary in different localities and also be largely influenced by weather. In America, the flowers are reported to open by night but the time is not recorded. In Gujarat, the flowering commences from 4 a.m. and is confined to the forenoon. At Nagpur, the flowering starts by 11 p.m. and continues upto 4 p.m. next day. At Bellary, flowering is reported to be between 1 a.m. and 4 p.m. At Coimbatore, *Sorghum Roxburghii var. hians* and *S. nervosum* commence flowering at midnight to 2 a.m. *S. durra* starts late by 4 a.m. and finishes by 8 a.m. Wet weather delays blooming as well as bursting of anthers. *S. margariferum*, a species introduced from Sierra Leon, is the only type that blooms from 8 a.m. to 4 p.m.

The table gives the details of flower opening at Coimbatore :—

TABLE 73.

	0—2 A.M.	2—4 A.M.	4—6 A.M.	6—8 A.M.	8—10 A.M.	Total No. of flowers.	Total No. of days of flowering.
S. Durra : Periamanjal cholam.	1620	1693	238	13	...	3564	9
S. Roxburghii : Talaivirichan cholam.	3235	850	17	5	...	4107	8
S. nervosum : Irungu cholam.	1511	365	14	9	2	1901	9

The maximum amount of flowering is over within the first three hours from the start.

Details of different steps involved in the opening of a typical flower have been furnished by the same authors.

TABLE 74.

Hours.	Minutes.	Seconds.	
2	...	... A.M.	Glumes begin to open.
2	1	... "	Staminal column just visible.
2	1	30 "	Staminal column completely visible.
2	2	... "	Stamens separate.
2	2	30 "	First anther tilts down.
2	2	40 "	First anther pendent.
2	3	... "	Other two anthers tilt down.
2	3	20 "	Other two anthers pendent.
2	18	..	Glumes begin to close.
2	45	..	Glumes completely close.

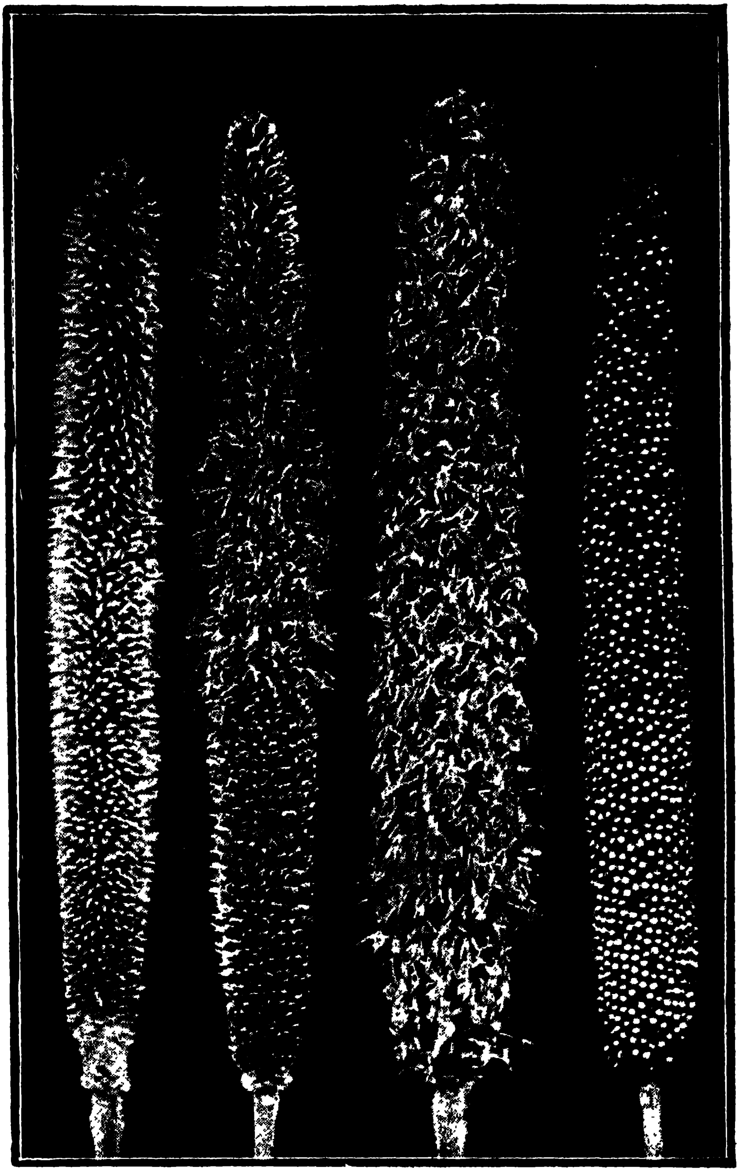
Observations by others show that this period may extend from 2 to 4 hours. Glumes open by the swelling of lodicules. The anther column comes out enclosing the stigmatic branches. The anthers may burst on appearance or after becoming pendent. The glumes close slowly and do not open again. The anthers are the first to begin to dry up by 10 a.m. and the stigmas begin to dry soon and both of them are dried up by next day. It has been pointed out that in *Sorghum* the spikelets occur in twos, one sessile and the other pedicelled. Some sessile spikelets may bear two pedicelled ones and the proportion of such spikelets varies as indicated in Table 75 :—

TABLE 75.

	% of with 2-pedicelled flowers to total.	% of pedicelled spikelets with anthers to total pedicelled spikelets.
Sorghum Durra	46	2·2
S. Roxburghii var. hians ...	34	*Nil.*
S. nervosum	29	*Nil.*

Almost all the pedicelled spikelets are barren but in some species they may be antheriferous as indicated above. Where stamens are present in pedi-

celled flowers, they emerge later than those of hermaphrodite flowers and the glumes keep open for a long time.



(*With the kind permission of India Government from Ind. Jl. Agri. Sc.*)

Fig. 120. Blooming in pearl millet (*Pennisetum typhoides*) (1) Protogyny, (2) first flush of anthers, (3) Dry anthers, and (4) grains.

3. **Pearl-Millet** (*Pennisetum typhoides*).—The inflorescence is a spike with a prominent central axis bearing rachilla and the latter in turn bears

ordinarily two spikelets. The spikelets are surrounded by a whorl of bristles. Blooming is throughout day and night. Observations at Coimbatore taken at 2-hour intervals are given in Table 76:—

TABLE 76.

		Total of 4 earheads
6 A.M.	...	598
8 ,,	...	539
10 ,,	...	735
12 NOON	...	480
2 P.M.	...	310
4 ,,	...	255
6 ,,	...	425
8 ,,	...	1122
10 ,,	...	1575
12 MID-NIGHT	...	1309
2 A.M.	...	1126
4 ..	...	706

While the heaviest anthesis is prior to midnight followed by a slight rise by 10 a.m. the weakest is by 4 p.m. The earhead takes about 8 days to complete flowering and largest number of flowers open on second day.

This crop is protogynous. The stigma takes a long time to protrude and open out, the time varying from 12 *to* 24 *hours, depending upon weather. It remains fresh for a similar period.* From the time anther tip is visible upto complete emergence it takes 1 to 2 hours and in 25 minutes the anthers dehisce. Absence of lodicules seems to be the cause for the slow and protracted anthesis and the pencil of tuft of hairs on anthers seems to help to a little extent in this process. The stigmas first emerge out and this proceeds from the tip downwards. Before this is completed at the base of the earhead, the emergence of stamens of bisexual flowers starts from the tip downwards and this starts 2—3 days after the first emergence of the stigma on the earhead. Again before this is complete at the base the second flush of emergence of anthers from staminate flowers starts from the tip downwards and overlaps the first flush. (Fig. 120).

High humidity and low temperature favour maximum anthesis in this crop.

3. **Ragi** (*Eleusine Coracana*).—It takes 5 days to complete flowering. In open type of fingers flowering starts from 1—2 a.m. and is finished by 3 a.m. In top and in-curved fingers, it starts by 2—3 a.m. and continues upto 5—6 a.m. with maximum between 3—4 a.m. Receptivity of stigma is shortlived and is upto 5 hours.

4. **Tenai** (*Setaria italica*).—Maximum number of flowers open between 10 p.m. and mid-night and between 6—8 a.m. The flower opening continues from 10—15 days. Humidity and temperature are the chief controlling factors.

5. **Kudiraivali** (*Echinochloa frumentacea*).—Flowers open from 5—10 a.m. with maximum between 6—7 a.m. The panicle takes 10—14 days for emergence and the flowering is tip downwards. It takes 19—22 days for completion of flowering. The flowers close in half an hour and these are mostly self-pollinated.

6. **Panivaragu** (*Panicum miliaceum*).—Flowers open between 10 a.m. and 12 noon. It takes 10 days for the panicle to complete flowering.

7. **Samai** (*Panicum miliare*).—At Nagpur conditions, the flowers open between 9-30—10-30 a.m. and they close in 15—20 minutes. They are mostly self-pollinated. At Coimbatore, the flowers open from 9 a.m. to 12 noon.

8. **Varagu** (*Paspalum scrobiculatum*).—At Nagpur, 5% of flowers only open and the rest are cleistogamous. They open from 7-30 a.m.- 8 a.m. and remain open for 20 30 minutes only after which they close. They are mostly self-pollinated. At Coimbatore, it is observed that the flowers begin to open from second day of emergence. They open from 2-30 to 3 a.m. Flowering starts from the middle and spreads to either end. Stigma may or may not protrude. By 3-45 a.m. the flowers close again. All flowers do not open and hence are cleistogamous.

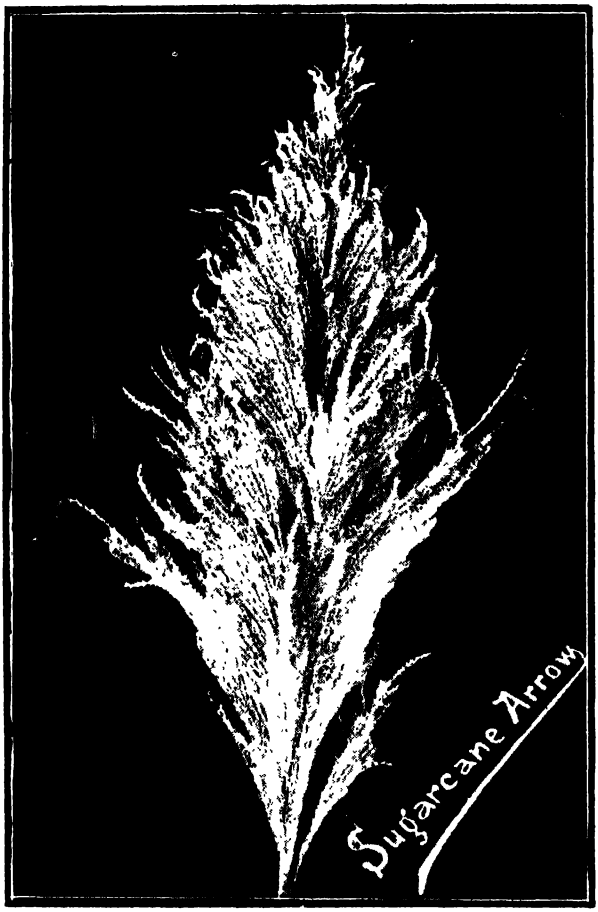
9. **Wheat** (*Triticum sp.*).—The blooming starts some days after emergence. The main culm flowers first and the tillers bloom later in the order of their formation. Flowering starts at a point two-thirds from the base and proceeds in both the directions. Blooming is noted throughout the day and it takes 3—5 days for completion. The glumes may fall apart within 20 minutes due to the rapid swelling of the lodicules.

10. **Barley** (*Hordeum vulgare*).—There are two maximum periods in a day, *viz.*, 6—8 a.m. and 3—5 p.m. It takes 7 to 9 days for the completion of flowering in a single plant. In some types cleistogamy is noticed.

11. **Sugarcane** (*Saccharum officinarum*).—Flowering in sugarcane is seasonal and seldom occurs outside the tropics. In northern hemisphere, flowering is in winter months of October-December and in Southern hemisphere from May-July. Some varieties flower regularly while others do not. In some varieties either of the sexes is not functional and hence they may be male or female from functional aspect. Few varieties are completely sterile. Sterility of male or female sex may change with locality as it happened with *Saretha* which was first male sterile but later at Coimbatore proved female sterile. The flowering of sugarcane is termed *arrowing of sugarcane*. The "arrow" is an open branched panicle. (Fig. 121). Spikelets are in pairs. Complete emergence of arrow may take 7 to 14 days depending upon the variety. The opening of flowers starts at different stages of emergence of the arrow in different varieties. It is soon after emergence in Vellai, Glagah and D. 74 ; at half emergence in majority of varieties and at full emergence in P.O.J. 2725. It takes 8 to 10 days for completion of emergence and flower opening.

There are two types of spikelets—sessile and pedicelled. The sessile flowers open first in *Saccharum officinarum* and pedicelled ones in *S. spontaneum*,

In the latter, flowers open by 6–55 a.m. Flowers of Sugarcane—Sorghum hybrids open by 3–45 to 4–35 a.m. ; those of P.O.J. 2878 show protracted opening.



(*Photo from Sugarcane Expert*).

Fig. 121. Sugarcane arrow.

12. **Maize** (*Zea mays*).—This is a monoecious plant. The *tassel* bears the male flowers and the *cob* or ear bears the female flowers. In the tassel, blooming starts near the tip in the central axis and then it progresses upwards and downwards. The upper florets are the first to bloom and before they finish blooming, a second flush by the blooming of lower ones is noticed. Blooming may be finished by noon and a tassel takes upto 14 days to complete flowering. Pollen grains are not emptied all at one time since the dehiscence of anther lobe is by a short slit at the tip. The pollen grains are viable for about 24 hours. A tassel may produce 20—50 million pollen grains which approximates to 45,000 pollen grains for each ovule. Anemophily is the commonest pollination type though insects may visit the flowers.

The cob bears the female flowers and it is enclosed in ' husk '. The style which is long and fine is termed ' silk '. In the cob, older flowers are at the

base and the silks of these are the first to elongate and they progress upward until they emerge out of the husk. The emergence of silks from all flowers may be completed in 2—5 days and the stigma is receptive for about 14 days.

In majority of the types, the flowers are dichogamous, though homogamous types are also found. It is essentially a cross-pollinated crop.

13. **Cotton** (*Gossypium sp.*).—In the time of opening there is much variation within variety. American types open earlier than the Asiatic types. Except in *G. religiosum*, the anthers dehisce after corolla opens. In Asiatics, majority of the types open between 8—10 a.m. Atmospheric temperature affects flower opening while humidity does not.

14. **Tobacco** (*Nicotiana tabacum*).—The anthers are below the stigma in the bud, but before the flower opens, the filaments grow rapidly and the anthers are pushed up past the stigma. They burst before the flower opens and thus self-pollination takes place to a large extent, cross-pollination being occasional.

15. **Black gram** (*Phaseolus mungo*) and Green gram (*P. aureus*). -Anthesis in these two crops was studied in the Godavari District (Madras). The anthers are the first to dehisce by 9 p.m. and this is completed by 3 a.m. Corolla is shed by the following morning. Since the pollen shedding takes place long before the petals open out, self-pollination is the rule in these crops. Cleistogamy is prevalent upto 46%.

16. **Bengal gram** (*Cicer arietinum*).—Active blooming is between 9-10 a.m. and proceeds upto 3 p.m. The flowers open on two successive days and on the second day, the opening is earlier and the process is over by 11 a.m. Some flowers do not open at all and the percentage of such cleistogamous flowers was 8—12 in winter months and 32—42 in summer months. Anthers dehisce 40 hours prior to flower opening and self-pollination is the rule, though cross-pollination may occur.

17. **Groundnut** (*Arachis hypogaea*).—The flowers are papilionaceous. There are 8 monadelphous dimorphic stamens. The anthers dehisce by 5—6 a.m. and the flowers open from 6—8 a.m. The crop is purely self-pollinated.

The flower buds appear in leaf axils either solitary or in clusters of 2 to 5. The flowers open in acropetal order. They are protected by bracts. Flowering period lasts from 45 to 60 days in bunch types and 60 to 70 days in spreading types. These periods are affected by distribution of rainfall. For pod formation, the gynophore which elongates in 4–5 days after fertilisation must reach the soil. In an experiment where the gynophore was allowed to develop in a medium of saw dust or inside a bamboo tube, pod failed to develop.

18. **Gingelly** (*Sesamum Orientale*).—The plants begin to flower in 25–40 days after sowing. Where the flowers are solitary, the blooming is racemose and where the flowers occur in clusters, it is cymose. The anthers begin to dehisce by 2–30 a.m. and the maximum is by 3–4 a.m. before the flowers open. The flowers open from 5–8 a.m. and it takes 2 hours for the corolla to open. It is generally shed by 6 p.m., though it may be macrescent in some. It is

mostly self-pollinated though cross-pollination is effected to some extent by the visiting butterflies, flies and bees. The stigma is receptive upto 7–8 a.m. on blooming day.

19. **Coconut** (*Cocos nucifera*).—The tree is monoecious and bears a large number of male flowers with a few female flowers at the base of the spadix. Variations in the appearance of successive spathes, the rate of splitting etc., vary with the season. It was observed by the reporting authors that (1) the period between two spathes is 18 days; (2) the period between the appearance of spathe and its splitting is a minimum of 104 days; (3) it takes 16–23 days for male flowers to open; (4) pollen grains are viable from 6–10 days; (5) self-pollination is possible.

20. **Brinjal** (*Solanum melongena*).—The flowers may be solitary or in clusters, and in the latter the first flower is always bigger than the rest. The opening of flowers and the dehiscence of anthers go together and this is later in winter months than in summer months. High temperature and high humidity in the morning hours tend to hasten while low temperature and low humidity tend to slow down flower opening and dehiscence of anthers. In winter, maximum opening is between 11—12 a.m. Flowers begin to close by 4 p.m. and this is completed by 10 p.m. The flowers open and close for a period of 8—10 days successively. In summer months maximum opening is on the second day. Stigma is receptive from 2 hours after flower opening and remains so upto third day. Dehiscence of anther is influenced by temperature and humidity. Dehiscence is irregular ; even two lobes differing in the time of dehiscence. Pollen is viable for 2 to 3 days under field conditions.

Length of style varies in the same plant and when it is below 0.58 cm. setting is nil. In longer styles (above 0.68 cm.) setting is best. In winter months larger percentage of short styled flowers are produced.

21. **Chillies** (*Capsicum annuum*).—In bud, the pedicel is erect but when the flower is mature it is bent. In Bihar, flowering begins by September and continues upto February. In November, buds open by 7-30 a.m. and continue upto 1 p.m. and the maximum is between 8-10 a.m. The flowers that open late do not open out completely and they fully open out the next morning. These are the first to open out the following day. The blooming is as noted in Table 77.

TABLE 77.

		No. of flowers.
7-30—8-30 A.M.	...	7
8-30— 9-30 „	...	52
9-30—10-30 „	...	33
10-30—11-30 „	...	14
11-30—12-30 P.M.	...	6
12-30— 1-30 ..	...	2

The length of style varies in the same plant. The style is curved to varying degrees and this curved position helps in self-pollination. Anthers burst and shed the pollen grains half an hour after flower opening and this interval may extend upto 5 hours. In this period, cross-pollination may take place.

Flowers remain open for 2—3 days and do not close at night. In some places, they are reported to close. The corolla is shed in 2—6 days.

22. **Jute** (*Corchorus sp.*).—From the time the floral bud appears, it takes 15 days for *C. capsularis* and 11 days for *C. olitorius* to open flowers. The hours of opening and closing of the flowers are shown in Table 78 :

TABLE 78.

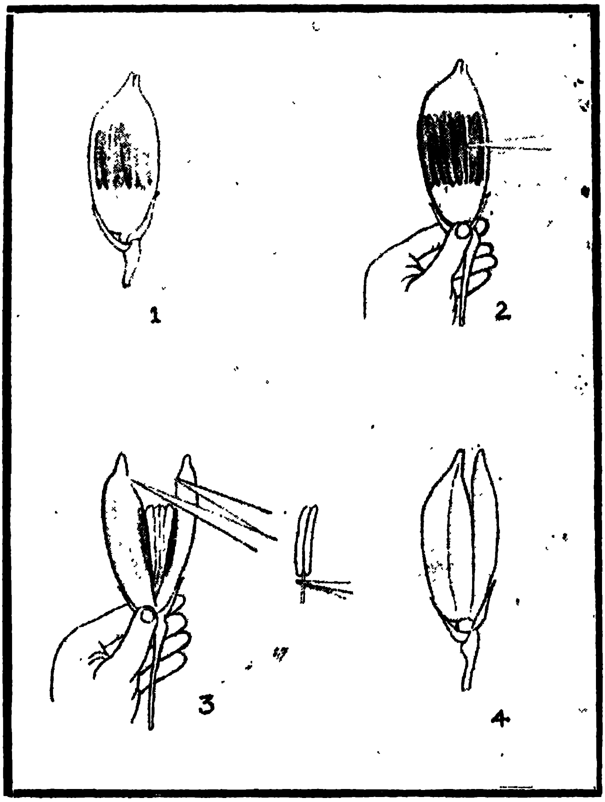
Species.	Opening.	Closing.	Remain open for.
C. olitorius (cultivated)	5-30—8 A.M.	1-30 P.M.	7 Hours.
C. olitorius (wild)	7 30—9-30 „	2 „	5½ „
C. capsularis	9—10-30 „	3 30 „	6½ „
C. acutangulus	11-15—11-45 A.M.	3-30 „	4 „
C. fascicularis	11-30—12 NOON	3-30 „	3¾ „
C. trilocularis	1-30—2 P.M.	5 „	3¼ „
C. tridens	2 15—2-45 „	5 „	2½ „

4. **Emasculation.**—When the flowers are hermaphrodite, the removal of stamens sufficiently in advance of the dehiscence of the anther sac is necessary if it is programmed to cross-pollinate the flower with the pollen of a known parent. The process of removal of stamens is termed *emasculation*. This is done a few hours before the flower opening or before the anthers dehisce whichever is earlier. This is done to prevent self-pollination. If the flowers are unisexual—monoecious or dioecious, the female flowers are protected by a suitable covering, long before the stigma is protruded and is receptive. The flowers on the male parent in all cases, are also similarly protected with the object of preventing foreign pollen falling on the flowers and thus contaminating.

The process of emasculation though essentially simple and consists in the removal of stamens, requires different field technique depending upon the ease with which it could be effected. The protective parts of flowers, *viz.*, bracts, sepals and petals are either removed or carefully opened out and then the stamens are removed. In this operation, care should be taken not to injure the flower as such a shock increases the chances of shedding of the flower. The technique adopted in the case of a few crops is discussed here.

Rice.—With the aid of forceps, the lemma and palet are gently opened out and the six stamens are removed by scissoring. (Fig. 122). This is done one to two hours before the normal time of anthesis in the variety. When sufficient number of flowers have been emasculated the rest of the spikelets are removed with the object of preventing the pollen from them falling on to the

stigma of emasculated flowers. The earhead is labelled and is enclosed in a muslin bag which latter is suitably supported on to bamboo stakes. (Fig. 123). This is to prevent contamination of emasculated flowers by foreign unknown pollen.



(*With the kind permission of India Government from Agrl. Jl. India.*)

Fig. 122. Emasculation in rice.

In Philippine and Java, the top half of the flowering glumes are cut off and the stamens are removed. At Coimbatore the flowering glumes are gently forced open by forceps. In rice, the extrusion of anthers is conditioned by temperature and not so much by moisture. Therefore the following device is adopted.

The panicle is enclosed in a brown paper cover 1½ to 2 hours prior to blooming time and the temperature inside the cover rises. At the optimum temperature, the anthers are extruded but they do not dehisce then. This generally happens in 15—30 minutes. They are then scissored off.

In many cases the factors governing the extrusion of anthers are different from those for the bursting of anther. These factors are not completely understood, and a knowledge of the same will be helpful in emasculating small flowers.

Ragi.—A method by which emasculation in this crop is made easy is reported from Mysore. This may be tried in other crops too.

Wide test tube or small flask lined with moist filter paper is inverted over the flower and plugged with absorbent cotton. After some time, anther sacs come out in tact without shedding pollen grains. They are then cut and removed.

(Photo from Paddy Specialist.)

Fig. 123. Rice plants covered with muslin bags to prevent cross-pollination.

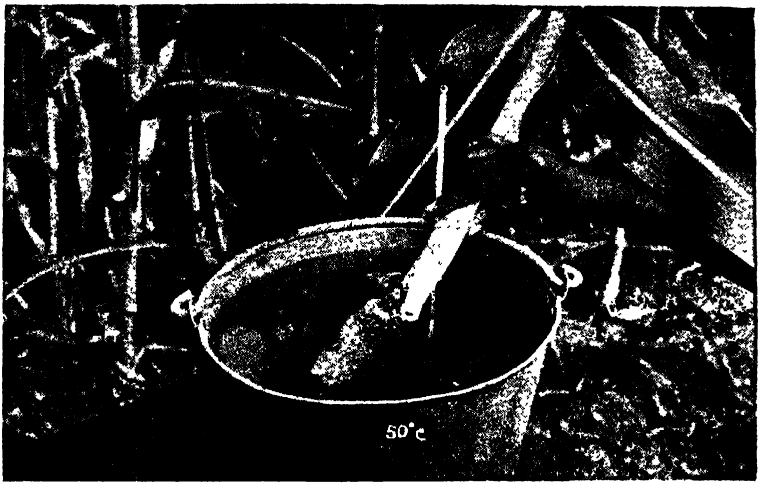
Sorghum and other grasses.—Another method for mass emasculation of small flowers, which can be tried with some success is as follows :

A large tin can is taken and a hole large enough to pass over the earhead is cut at the bottom. A section of tyre inner tube about 10″ long is stretched over the bottom of the can and when in use, the other end is secured to the peduncle. This can serves the purpose of water container. The can is mounted on a tripod. Water at 50°C is poured in the container and if the treatment lasts for about 10 minutes it is found that the pollen is killed. The temperature and duration for different plants may be worked by preliminary experiments. This hot water method for mass emasculation in *Sorghum* as adopted in Coimbatore is shown in Fig. 124.

Bengal gram.—Anthers dehisce 40 hours prior to flower opening. Flower buds which are likely to bloom two days hence are emasculated. In the evening keel is gently pushed apart with a bent needle and the anthers are removed by jerking them at the point of attachment with filament. The emasculated flowers are artificially pollinated the next morning.

Gingelly.—In short duration varieties, the flowers open earlier than in late ones. Anthers dehisce from 2-30 a.m. and the maximum dehiscence is by

3—4 a.m. and therefore emasculation is carried out the previous evening. A ' V ' cut is made at the dilated part of the corolla and the anthers are removed. Stigma is pressed in upper part of the corolla and therefore no damage is caused to it by this operation. After removing other buds that are likely to open the following day the entire plant is covered for protection against contamination by foreign pollen.



(*Photo from Millets Specialist.*)

Fig. 124. Emasculation of *Sorghum* spikelets by hot-water method.

Ground-nut.—Since the anthers burst by 5 a.m. emasculation is carried out the previous evening. The floral parts are carefully opened out and the stamens are removed. No covering is necessary in this crop as they are always self-pollinated and the floral parts protect the stigma from any such danger.

Castor.—Since the plant is monoecious emasculation is easy and consists in the removal of the male flowers which are borne at the base of the inflorescence. In some stray cases, occurrence of male flowers amongst the female ones may be noticed and these are also to be removed.

Coconut.—This is also monoecious. The spadices are to be covered by a close-meshed cloth bag ten days after spathes open out. Male flowers are removed 8—10 days before the female flowers open out. The pollen grains are viable for 6 days and hence the female flowers are protected with the cloth bag for 15 days after artificial pollination.

Chilly.—Since the flowers open out in the morning, emasculation is carried out the previous evening. The buds may be opened out and the stamens cut and removed. One easy method of emasculation is to gently pull out the corolla. The stamens are epipetalous and therefore they are removed along with the corolla. When sufficient number of flowers are emasculated, the other buds which may open out the next day are removed and the entire plant is covered with a muslin bag.

In all cases, when emasculating, care must be taken not to puncture the anthers and thus shed the pollen grains. After emasculation is over and before covering the individual flower or the entire plant, the stigma of emasculated flowers must be carefully examined with a hand-lens for the presence of any stray pollen grain. If the stigma is contaminated, it is safe to reject the flower.

As has been already mentioned, whenever possible, the emasculated flowers are labelled for later identification. In cases where individual flowers are too small to be labelled as in rice, a label is tied to the rachis of the group of flowers which have been emasculated and crossed. In such cases, all other flowers are removed.

In such of the cases where the flowers are perfectly male sterile, or self incompatible, emasculation is not necessary. Such is the case with self sterile sugarcane varieties as Co. 281 and male sterile varieties as P.O.J. 2725 and Vellai.

5. Artificial pollination.—The flowers on the female and male parents are now properly protected. In the male parent, such of the flowers as are likely to shed their pollen grains when the stigma of the emasculated female parent becomes receptive, are chosen. At the time when anthers dehisce, pollen grains are collected in suitable containers and by means of fine brush are dusted on to the stigma of the female flower.

In the case of sugarcane, where there are male sterile varieties, the arrows are protected by fine muslin bags. When the anthers of the selected male parent dehisce, the arrow is cut and enclosed within the same bag as the female parent. The pollen grains shed on the female and crossing is naturally effected.

6. Natural Crossing.—In nature, there are various pollinating agents such as wind, insects, etc., and these cross-pollinate unless the floral adaptation is such that self-pollination is the rule. For a plant breeder a knowledge of the extent to which natural crossing takes place is necessary. It is useful in judging how far the purity of his improved types can be maintained under natural conditions. Further, the extent of heterozygosity and variability in natural population depends upon the natural crossing prevailing in nature. Breeding programme is necessarily based on such variability.

This is estimated by planting in adjacent rows pure-breeding varieties which show distinct differences in respect of known characters. Any variation in the characters, which are easily detectable in the first generation itself, denote natural crossing from adjacent rows. Another method by which this could be tested is to emasculate a large number of flowers and leave them for natural cross-pollination. From the setting of fruits, the extent of natural crossing can be judged.

Natural crossing or vicinism is variable depending upon environmental conditions. If the pollinating agents are active, it may increase. This in turn depends upon weather conditions and geographical situation. Therefore,

in respect of any crop varying degrees of natural crossing have been recorded from different research centres. As an example, the reports on natural crossing in rice in different countries indicate it to be of varying degrees as shown in Table 79.

TABLE 79.

Place.	Natural cross percentage.	Remarks.
Lower Bengal ...	4·0	
Burma	1·1	
Central Provinces ...	0·1 to 2·9	In cultivated types.
	7·9	In wild types.
Madras	2 to 4	
	15 to 20	In hybrid progenies of wild rice.
Bombay	0 to 4·31	Average : 0·52
Japan	0·21 to 2·32	
Formosa	0·9 to 1·45	
Java	1·3 to 4·0	As much as 23% in some cases
Philippines ...	2·4	
Ceylon	0·34 to 0·67	
Australia	0·44	
America	0·45	

The average percentage of natural crossing in respect of other crops is shown in Table 80.

7. Culture of parents.—When a breeder embarks on large scale hybridisation programme, the work is made efficient by the adoption of proper technique in emasculation and artificial pollination. In some cases it may be expedient to use the plants where they are naturally growing and separate culture of the plant in another place may not be easy. This is the case with shrubs and perennial fruit trees. Much time may be consumed in the breeder's visit to these plants for carrying out the various steps in hybridisation. Therefore it is necessary to raise such of the parents as are required for hybridisation work in a compact area. In crop breeding stations, wherever feasible, separate breeding plots may be raised, where all the parents required for hybridisation work are suitably planned and sown to increase the efficiency in cases of large scale hybridisation programme. In some cases, the two parents chosen for hybridisation may not come to flower simultaneously. In such cases, the breeder has to device methods to make the male and female parents flower simultaneously or to preserve the pollen grain until such time when the stigma will be receptive.

TABLE 80.

Crop.	Natural cross percentage.	
Cholam	25	
Wheat	5 to 6	It may be high in some varieties, but highly variable between varieties.
Barley	Rare	
Castor	5 to 14	
Ground-nut ...	*Nil.*	
Gingelly	6	
Panicum miliare ...	*Nil.*	
P. crusgalli ...	*Nil.*	
P. scrobiculatum ...	*Nil.*	
Cotton	5	
Jute ...	Over 2.	

When two parents differ in flowering duration only, the planting time may be so adjusted as to make them flower simultaneously. In these cases, the planting of the crop is so adjusted that the two parents come to flowering at the same time. As an example, the influence of planting time on the flowering duration of pure line T. 24 rice is given in Table 81.

In the same crop, wider spacing between plants delayed flowering as also the high fertility of the field. At Coimbatore, the problem of making different parents flower at the same time is solved by adjusting sowing dates and cutting back the later ones to induce secondary tillering. If the flowering cannot be made to synchronise by this method, one of the parents is either artificially forced to flower or the other is retarded in this process. Though flowering duration of many crops is genetically controlled, it is also largely subject to environmental conditions. In Japan and Burma, the flowering is adjusted by reducing the period of sunlight which forces the plant to flower earlier.

In sugarcane, the time of flowering may be altered to a certain extent by photo-periodic effect.

Saccharum spontaneum from Burma was subjected to the following treatments : The plant in pots were exposed to day-light for 2 hours only between 12 noon and 2 p.m. and kept in darkness for rest of day. This treatment was continued for 2 months. Such treated plants flowered three weeks after treatment while other plants receiving 10, 14, 22 hours and normal day-light did not flower at all. *S. spontaneum* (Assam) flowered with 9 hours day length.

In P.O.J. 2725, flowering was delayed by a month when subjected to 18 hours day length. In the same type, flowering was prolonged upto the end of December while the controls cease arrowing by the end of October.

TABLE 81.

Sowing date.	Flowering duration in days. 1925–26.	1927–28.
June 1st ...	138	...
July 1st ...	118	113
August 1st ...	98	98
September 1st ...	90	85
October 1st ...	94	88
November 1st ...	91	116
December 1st ...	95	98
January 1st ...	104	130
February 1st ...	224	231

In the case of perennial plants, a number of horticultural methods are known, chief of them being, the different methods of pruning. Treatment with volatile chemicals such as ether, acetone, ethylene, etc., also force the plant to bloom. Injection of water or salt solutions, treatment with hot water, exposure to X-ray, freezing, are other methods adopted in forcing plants to bloom.

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Fig. 125. Sugarcane arrows cut for hybridisation work.

Hybridisation of plants which flower with short interval between them can also be done by preserving the pollen until the female parent comes to flower.

Pollen has been successfully preserved in some cases under artificial conditions for some weeks. Optimum conditions and the maximum period for which any one variety can be preserved must be tested. In general, the pollen of dicotyledons can be preserved for longer periods than the pollen of monocotyledons. An ingenious method has been devised for preserving the pollen of sugarcane.

The arrow is cut early in the morning. Cane portion is dipped in a bucket of water and another cut is made under water. (Fig. 125).

Clay is stuck to the cut end. The arrow is wrapped in tissue paper and then with brown paper. It is then closely wrapped in straw and packed in bamboo crates. The arrow lasts for 11 days and the pollen are viable. An advantage in this method is that it stands long distance transport.

Chapter 19

NEW SELECTIONS BY HYBRIDISATION

INTRODUCTION—CHOICE OF PARENTS—CROSS-POLLINATED CROPS—CLONES—HYBRID VIGOUR—INTERSPECIFIC AND INTERGENERIC CROSSES—BACK-CROSSING—SELECTION IN HYBRID PROGENIES—LIMITATIONS—ACHIEVEMENTS

1. Introduction.—For a long time selection from naturally existing population was the only method adopted for improvement of cultivated crops. Selection was practised either in the local bulks or by introducing new bulks from other areas. These methods, though highly useful, have not been sufficient enough to satisfy the ever increasing demands of the modern civilisation. A large number of useful and desirable characteristics of field and garden crops, such as drought and disease resistance, yield, quality, etc., are not always found combined in one single type. The agriculturists and on his behalf the plant breeders want a single type that will combine in itself all the desirable qualities. When Mendel established particulate inheritance, the factors governing the different characters of a plant were seen to be inherited independent of each other. This was taken as a good augury, since it was hoped that all the desirable characteristics of crop plants could be easily recombined by hybridising the parents possessing them and then selecting in the hybrid progenies. It was first taken to be as easy as that of dismantling and assembling parts of machines of the same make. Later experiences in this direction proved the limitations of this hope, though very important and very useful progress have been made both in the selection of highly desirable types and in acquiring more knowledge of the problem. In many cases new selections were made without particular knowledge about the genetics of the parents or the individual character but wherever the latter were available the task of selecting improved types was considerably more efficient. It must be borne in mind by every plant breeder that greater and continued advancements in practical selections of improved types could be made only with the knowledge of the genetics of the characters, and of the species and allied plants and any advancements due to chances should not detract them from the study of the fundamentals of the science. Some aspects of the problem of hybridisation are discussed in this chapter.

2. Choice of parents.—This is one of the most difficult steps for decision by a plant breeder. Before embarking on a programme of hybridisation, the consideration of the following two points is important (1) all the requirements of the tract, either from agriculturists' or industrialists' point of view must first be listed. Variations in soil, climate, agronomic practices, market conditions and industry are varied enough to make it difficult to evaluate

the problem ; (2) a survey of the existing types in the tract as to how far they satisfy the requirements and their utility as parents in hybridisation.

A thorough investigation as to the objects with which a selection or hybridisation programme is embarked on, is necessary. Based on this information, the important characteristics desired are listed. A search is made in the bulk populations of the tract for single plants that may combine all or a few of the desired characters. If no single type meets all the requirements, hybridisation is resorted to recombine the characters found in two or more types. If no desirable parents are available in the tract, a survey is carried out in adjacent tracts or other similar geographical areas where the crop is cultivated under similar agronomic conditions. Failing to secure parents locally, one should turn to primary or secondary centres of origin where dominant wild genes and wide range of variations are existent. Parents may be chosen this way for hybridisation.

In selecting parents for hybridisation, evaluation of the parents as to their efficiency in yielding desirable progenies on hybridisation, is difficult for the various genetic considerations : (1) phenotype is no indication of the genotype. (2) developmental variations are large enough to mask genetic variations. (3) the behaviour of genes in different genetic back-grounds are different due to interaction, etc. (4) the character, if governed by a large number of genes, is complex in inheritance. (5) there are various limitations for free recombination of genes in the hybrid progenies.

As an example of the complications it may be stated that a parent proving useful in one cross may not prove equally so in another. In cotton, a cross between types 329 and 54 gave a higher proportion of economic types than the cross 329 × 2919 as shown in Table 82.

TABLE 82.

I Parent.			II Parent.			No. of F_2 plants examined.	Standard for selection.		Per-cent above standard.
Name.	Lint length.	Ginning per-cent.	Name.	Lint length.	Ginning per-cent.		Lint length.	Ginning per-cent.	
329	21	24	2919	20	27	3198	21	23	4·5
329	21	24	54	22	23	492	21	23	11·0
2919	20	27	Wagad 14	20	36	161	22	29	7·0
2919	20	27	H. 190	22	30	194	22	29	0·5

The same author gives an instance where the reciprocal crosses differed in their out-put of economic types. This is shown in Table 83.

TABLE 83.

Parent.	Parent.	Total F_2 studied.	Percentage of plants better than standard.
Co. 2	*A* 12–15	215	19
A 12–15	*Co.* 2	233	0
Co. 2	*A* 17–17	707	18
A 12–17	*Co.* 2	163	0
Co. 2	*U4 H77*	869	12
U4 H77	*Co.* 2	248	0

It is seen that crosses with Co. 2 as male parent have failed to yield useful types in the progeny.

Some parents may show differences in their behaviour in different tracts. Thus it is reported that the cross U4×cambodia failed to yield useful types in Rhodesia while the same cross-yielded types at Coimbatore. The behaviour in this instance may probably be due to heterozygosity attributed to U4 but such differences are not improbable.

In choosing parents, the following general considerations may be borne in mind.

The two parents should not be widely differing. Large differences between the parents, such as between two species, cause instability in genetic balance of the progenies. As far as possible, different ecotypes or geographical forms of the same species, or plants from similar climatic regions or neighbouring tracts are recommended. Genotypes may be built up by complex hybridisation such as by *multiple* and *cyclic crosses* but the process does not prove successful in all places. In the case of asexually reproduced crops, genetic instability in sexual organs is no barrier and crosses between different species and genera may be attempted as in the case of sugarcane. In the case of corn, *convergent improvement* by back-crossing and utilising the hybrid vigour have been adopted with practical success.

3. **Cross-pollinated crops.**—Reference was already made to these plants and it was pointed out that these are highly heterozygous. Therefore, if any uniform results are to be aimed at, homozygous types are to be evolved for purposes of hybridisation. Crossing between heterozygous types in cross-pollinated plants is not helpful for the reason that any useful progeny from such a hybrid cannot be maintained pure, or production of such a hybrid again becomes difficult due to the impossibility in maintaining the parental types which segregate and are thus lost. It was pointed out in chapter XVI that selfing or inbreeding in naturally cross-pollinated crops leads to reduction in vigour. Many abnormal types are thrown out in the first few generations and deterioration in vigour is rapid to begin with but after about ten generations of selfing, the plants reach stability and breed pure. These pure

lines by themselves are uneconomic. When these pure lines are crossed, highly productive and vigorous progenies are produced. Detailed work has been carried out in the case of maize where pure lines were established for utilising them as parents in hybridisation. The utility of a pure line lies in its ability to produce vigorous offsprings in crosses with other types. Utilisation of hybrid vigour in such crosses is discussed elsewhere.

4. Clones.—Selection within clones is without possibilities of improvement unless the population proves a mixture from genetically differing parents. When a clone is sexually propagated, the seedlings show wide variability due to segregation of heterozygous factors. Therefore, variability in normally asexually propagated plants can be induced by selfing the plants and sowing the seeds. Homozygous types may be established by continued selfing and selection. Improved types may be found in the seedling progenies. Hybridisation between the variable types of seedlings yields useful combinations. When a seedling with desirable characters is selected, further propagation is through vegetative means because, deterioration by segregation will set in if sexual propagation is adopted.

The improvements effected in sugarcane may be pointed out as an example. Details have been already discussed in chapter XVII and the variability in the seedlings has been pointed out. Another important feature in this crop is that it is highly polyploid and heterozygous. Due to its mixed origin, it crosses with plants, distant on the taxonomical scale. (Fig. 131). These hybrid seedlings, when economic, have been maintained and cultivated by vegetative propagation. Thus, the hybrid characters are fixed in clones and the same is impossible in grain crops.

In sugarcane, the plants are selfed by covering the arrows with muslin bags. The seeds from such arrows are sown to raise seedlings. Further progress was made by (1) crossing indigenous canes with imported types. (2) crossing cultivated types with wild canes. (3) crossing cultivated types with other genera (such as *Sorghum* and bamboo attempted at Coimbatore). Each seedling is the basis of a new variety. A perusal of the parentage of some of the renowned cane varieties will show the complex hybridity of these and the rapid progress in sugarcane improvement in India would have been impossible but for the vegetative propagation of the crop and the shrewd planning.

5. Hybrid vigour.—When two varieties are crossed, the hybrid is more vigorous than either of the parents. (Fig. 126). This is termed *hybrid vigour* or *heterosis*. This phenomenon was known to early hybridists like Gartner, Kolreuter and others. This was variously termed by them as " stimulus of heterozygosis ", " heterozygotic stimulation " etc. Shull (1914) suggested the term *heterosis* for this hybrid vigour.

It was first suggested by Jones (1917) that the increased vigour in the hybrid is due to favourable dominant factors coming together in F_1, while some of them in nature lie separated in the two parents. In quantitative characters, where large number of factors are involved, this is possible as

follows : AA BB cc dd ee × aa bb CC DD EE gives F_1 of the genotype Aa Bb Cc Dd Ee. If it is supposed that all the five dominant factors are favourable ones, the hybrid contains all the five favourable factors, while the two parents contain 2 and 3 factors respectively. In later generations the progenies

Fig. 126. Hybrid vigour in chilly (*Capsicum annuum*). The hybrid is in the centre with the two parents on either side.
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show deterioration due to segregation in these factors. Further, linkage relationships of the various factors set a limit to free recombination and formation of homozygous types that will exhibit increased vigour to the same extent as the hybrid.

East (1936) emphasised the roll of linkage and multiple alleles in explaining heterosis. Very large number of factors each with small and cumulative effect control most of the characters. It is supposed that the combination A_1 A_2 or A_1 A_3 etc., are more vigorous than A_1 A_1 or A_2 A_2.

Ashby (1937) analyses heterosis in three stages and concludes that increased embryo size or "greater initial capital" is responsible for heterosis. Though initial increase in embryo size was evident in the materials studied by him, the same is not found to be an universal phenomenon.

Recent studies in corn reveal another explanation for hybrid vigour. In dealing with the improvement of cross-pollinated plants, selection of selfed lines and further crossing between them were referred to. The selfed lines show different degrees of "*combining ability*" which latter connotes the increased production in in-bred variety crosses. Some in-bred lines when crossed together yield progenies, on selfing which latter, pure lines with high

TABLE 84.

YIELD OF GRAIN IN BUSHELS PER ACRE.

Year.	Inbred parents.		F_1.
	P_1.	P_2.	
1917 ...	5·5	21·5	64·5
1918 ...	23·5	26·9	120·6
1920 ...	27·8	16·2	127·6
1921 ...	13·1	19·6	72·8
1922 ...	26·1	20·0	160·4
1923 ...	21·0	13·2	61·0
Average ...	19·5	19·6	106·2

(*after Jones*).

yield are obtained. If the start is made with in-bred lines of low combining ability, selfing the hybrid, results in pure lines with low yield. These experiments of Hayes and Johnson (1939) places heterosis in the category of mendelian quantitative characters. This new interpretation gives a new scope for the practical application of heterosis in that, isolation of vigorous selfed progenies of cross-pollinated plants is made possible.

The increased productivity of the hybrid has been utilised in corn production. Table 84 shows the increase in yield when two inbred lines are crossed.

If the F_1 is selfed, vigour is rapidly reduced in successive generations as shown by the average yield in different generations as presented in Table 85.

TABLE 85.

	Yield of grain in bushels per acre.
F_2	69·1
F_3	42·7
F_4	44·1
F_5	22·5
F_6	27·3
F_7	24·5
F_8	27·2

In cases where propagation is by seed, increased yield of the hybrid can be taken advantage of by producing hybrid seeds every year on large scale. For this purpose, the inbred parents are also selfed every year and maintained pure. Both the parents are raised on large scale and by mass hybridisation, hybrid seeds are produced every year and distributed to cultivators.

In the case of vegetatively propagated plants like sugarcane, potato, etc., the F_1 is vegetatively propagated and hence the hybrid vigour is not lost.

In-breeding increases homozygosity of genetic factors. In the case of naturally cross-pollinated crops like maize, there are many harmful factors in heterozygous state. Under heterozygous state, the recessive factors cannot show their harmful effect, but on being rendered homozygous they begin to express themselves phenotypically. It is for this reason that the selfed progenies of maize are less vigorous and in the earlier generations of selfing, defectives appear. After few generations of selfing the plant becomes homozygous and breeds true. In the case of naturally self-fertilised crops like peas or beans, on selfing, such defectives should have appeared in the earlier years of evolution. Natural selection has eliminated the undesirable genes which have no selection value. It is now assumed that either by man or Nature, selection and elimination of defectives should render crops like maize behave like peas and beans on selfing. This may be possible, if a homozygous type with all the favourable growth factors is evolved. This can be done by crossing selfed lines, the process being repeated a number of times with types that show high combining ability. This results in progressive improvement in yield of the selfed lines and is referred to as *convergent improvement.*

Heterosis is observable in many characters such as height, size, productiveness, earliness, health, viability, etc. Allopolyploids, which are formed by the doubling of chromosomes in the F_1 of the hybrid of two species, are more vigorous than the corresponding diploids because they retain their hybridity permanently.

The value of heterosis is known since ancient days as is evidenced by the production of mules by hybridising the two species of *Equinus*—the horse and

TABLE 86.

HYBRID VIGOUR IN RICE.

Character.	T. 237.	T. 389.	T. 237 × T. 389.	T. 389 × T. 237.	T. 335.	T. 495.	T. 335 × T. 495.	T. 6.	P. 115.	T. 6 × P. 115.	P. 115 × T. 6.	T. 588.	M. 11.	T. 588 × M. 11.	M. 11. × T. 588.
1. Height of seedlings.	22·2	21·0	21·9	22·1	11·2	11·88	11·47	7·38	3·43	7·11	5·32	4·30	4·42	4·41	4·46
	(Age 27 days.)				(Age 17 days.)			(Age 8 days.)				(Age 10 days.)			
2. Tiller counts ...	23·8	33·3	29·7	27·9	20·79	21·60	23·71	9·51	7·55	14·25	13·05	19·07	12·93	18·50	15·84
	(Age 95 days.)				(Age 112 days).			(Age 106 days.)				(Age 105 days.)			
3. Number of ears per plant.	20·0	26·1	26·6	24·5	15·58	15·11	17·97	8·15	6·08	13·72	12·18	17·60	10·80	14·70	14·47
	(Age 131 days.)				(Age 147 days.)			(Age 145 days).				(Age 151 days).			
4. Height of plants (inches).	46·3	51·0	49·3	49·7	39·86	38·29	39·93	36·74	33·54	40·34	37·08	35·54	37·30	39·12	38·89
5. Length of panicle (cm.).	22·99	22·29	24·09	24·30	18·63	18·76	18·72	19·46	20·33	22·77	21·40	19·51	22·42	21·51	21·54
6. Yield of grain (gm. per plant).	60·40	72·80	93·80	89 95	15·58	12·66	16·92	16·78	6·84	20·55	17·15	24·84	18·75	29·29	28·70
7. Weight of grain (gm. per 100 grains).	2·50	2·83	2·69	2·70	1·51	1·79	1·66	3·04	1·10	1·24	1·23	1·80	2·05	1·83	2·04

the ass. The mules are sturdier than the parents and as such are largely used in military transport. Many of the commercial fruit plants are hybrids which are maintained by vegetative propagation.

The following are some examples of hybrid vigour in crop plants.

At Coimbatore hybrid vigour in rice was studied in four sets of crosses involving parents which differed in size of grain, rate of tiller production, flowering duration, height of plants, length of panicle, yield per plant, etc. These characters were studied in the hybrid and the data are presented in Table 86.

TABLE 87.

——	Mean height of plants cm.	Mean No. of stalks per plant.	Growing season.	Mean yield per plant in lbs.	
				Forage.	Grain.
F_1 showing maximum vigour.—					
Parents: Dwarf yellow milo...	142·7	2·8	105	1·32	0·44
Black hul Kafir ...	125·7	1·03	105	0·64	0·20
Hegari ...	150·1	2·9	125	1·61	0·36
Spur feterita ...	157·8	1·3	100	0·81	0·26
Dwarf broom corn.	109·0	3·6	105	0·79	0·20
F_1 Dwarf yellow milo × Hegari.	246·8	3·7	136	3·20	0·79
Dwarf yellow milo × B. h. Kafir.	277·1	2·8	136	3·05	0·69
B. h. Kafir × Hegari ...	313·7	3·3	153	4·23	0·88
Hegari × spurfeterita ...	296·8	3·1	153	3·92	0·80
Hegari × Dwarf white broom corn.	388·6	4·0	155	4·25	1·06
F_1 showing intermediate vigour.—					
Parents : B. h. Kafir ...	125·7	1·03	105	0·64	0·20
Spur feterita ...	157·4	1·3	100	0·81	0·26
Sumac ...	186·8	2·1	100	1·21	0·26
F_1 B. h. Kafir × Spurfeterita ...	188·5	1·8	97	1·55	0·59
B. h. Kafir × Sumac ...	188·3	1·8	100	1·35	0·41
Spurfeterita × Sumac ...	199·1	2·0	95	1·40	0·54
F_1 of closely related varieties.—					
Parents : Dwarf yellow milo ...	142·7	2·8	105	1·32	0·44
Dwarf white milo ...	135·5	3·8	105	1·56	0·53
B. h. Kafir ...	125·7	1·03	105	0·64	0·20
Red Kafir ...	127·5	1·03	105	0·69	0·10
F_1 D. Y. Milo × D. W. Milo ...	140·9	4·4	105	2·25	0·64
B. h. Kafir × Red Kafir ...	134·8	1·7	105	1·12	0·43
Crosses between inbred lines of B. h. Kafir.—					
Parents : Line 153 ...	122·1	1·1	...	0·74	0·18
Line 223 ...	120·3	1·1	...	0·77	0·14
Line 646 ...	115·9	1·2	...	0·87	0·14
Line 153 × 223 ...	118·6	1·6	...	0·94	0·19
Line 153 × 646 ...	121·2	1·5	...	0·86	0·20
Line 223 × 646 ...	119·1	1·4	...	0·93	0·16

(After Karper and Quinby).

In rice, the size of embryo is highly correlated with the size of grain. The data in Table 86 show that in rice the hybrids manifest heterosis even in such cases where the hybrid shows no increase in size in embryo or endosperm.

In cotton, seed weight by itself gives ample evidence of manifestation of hybrid vigour and is a good index in forecasting hybrid vigour in post germination period.

Hybrid vigour in *Sorghums* was studied by Karper and Quinby (1937). The degree of heterosis widely varied. Two varieties, Milo and Hegari, showed maximum hybrid vigour when they entered in the cross with any other variety but when they were inter-crossed the hybrid vigour was no greater because they seem to contain similar of the dominant genes. It is seen that the commercial varieties are recessive in many genes and varieties which are assumed to be closely related are really genetically distant ; *e.g.*, Hegari and Feterita came from Africa and showed the same complex of seed characters and also otherwise closely resembled but judging from heterosis they are widely different. There are other varieties which show intermediate type of heterosis. The expression is not by increased height but the yields of grain and straw are increased. To this group belong the varieties, *Black-hul-Kafir*, *spur feterita* and *sumac*. Though these types differ visibly the heterosis shows that they differ in few genes only. In the third group fall the closely related varieties like Dwarf-yellow-milo and dwarf-white-milo. The expression of heterosis is much less in this group and yield only is increased. The data of Karper and Quinby are presented in Table 87.

Though the hybrid yields more than the parents, sometimes even 2–3 times the parents, the difficulty lies in the fact that large quantities of hybrid seeds have to be produced every year. Since the flowers are small, large scale emasculation and crossing is not easy. The problem may be solved by mass emasculation methods, such as hot water treatment, adopted in cholam, or selection of male sterile plants as in sugarcane.

6. Interspecific and intergeneric crosses.—Genetic nature of species differences was discussed in Chapter XII. A true species is one which yields sterile hybrids on crossing with another. If this be the criterion, classification becomes laborious and difficult and therefore classification on morphological basis is adopted in the herbarium. The sterility in interspecific crosses arise due to structural differences in chromosomes of the two species. Complex changes may take place in the course of formation of a species from its

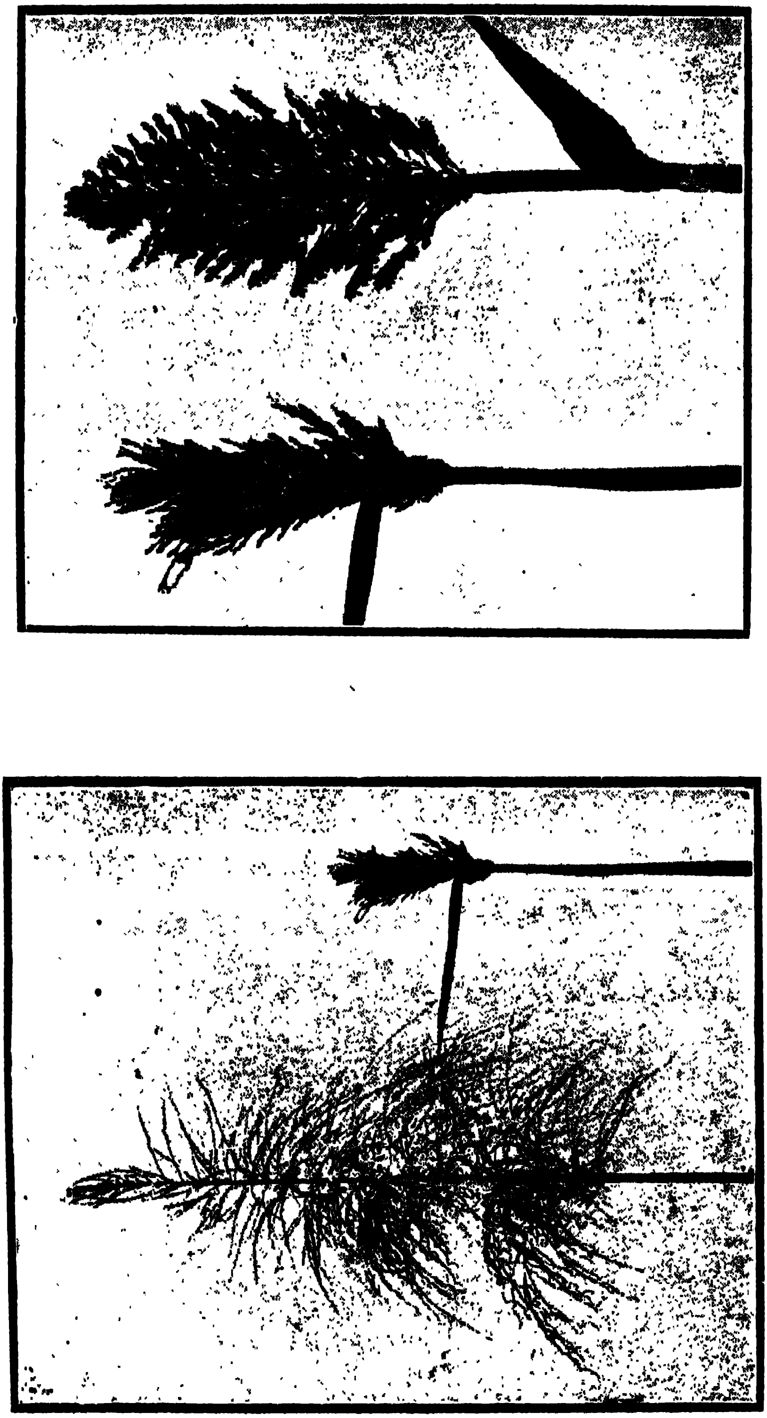

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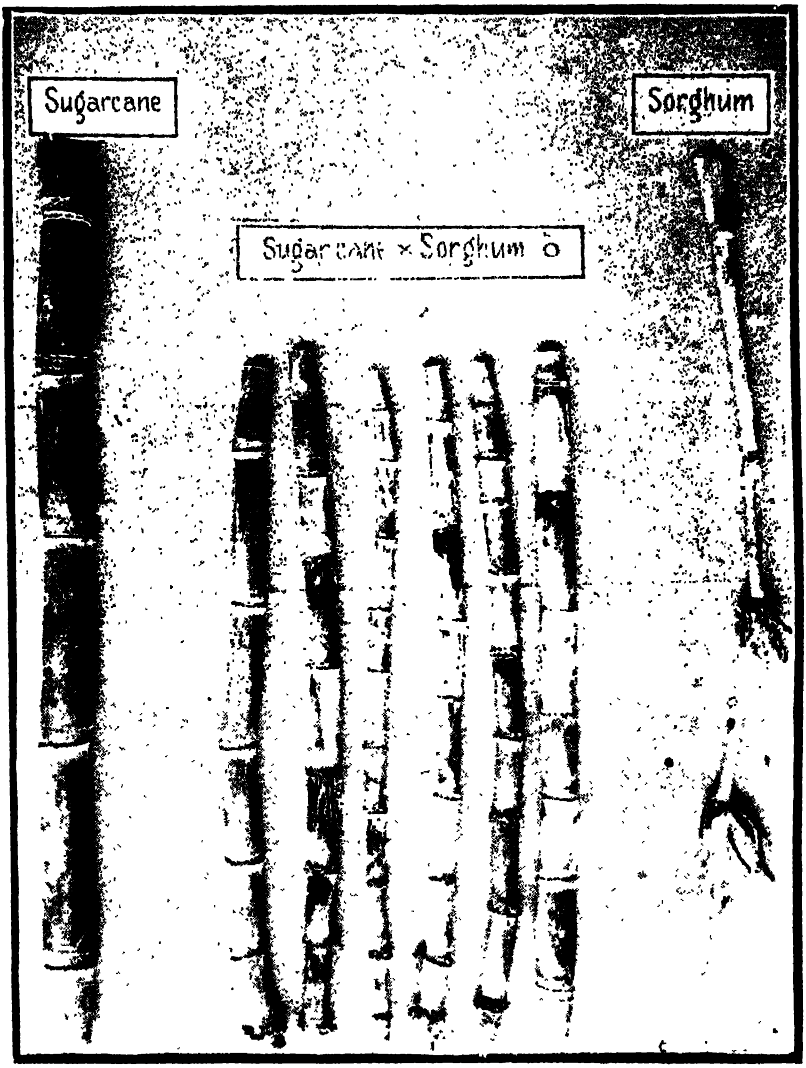
Fig. 127. Sugarcane arrow and Sorghum earheads with the hybrids in the centre.

progenitor. Since classification is mainly on morphological grounds, inter-specific crosses may either completely fail or the hybrid will show sterility to varying degrees.

A comprehensive knowledge of the genetic make up of a species is necessary if accurate planning of the species crosses is to be made. Next to *Drosophila*, it is only in maize that such an analysis has been attempted.



(*Photo from Sugarcane Expert.*)

Fig. 128. Sugarcane and Sorghum with the hybrids in the centre.

In cotton, the genetics of species development has been discussed by Harland and Silow. In the old world cottons the relationship of *G. arboreum*

to *G. herbaceum* is similar to that between *G. hirsutum* and *G. barbadense*. Many of the main loci are common but the modifier complexes differ. The interspecific hybrid, *G. arboreum* × *G. herbaceum* breaks down due to the fact that the genotypic make up of the hybrid is not stable. Therefore, so far as cotton is concerned, straight selection from species hybrids was not successful in yielding improved types. An exception is H. 190 of Mysore which is a selection from the interspecific cross *G. arboreum* × *G. herbaceum*.

Russian workers claim possibilities of selecting improved types from interspecific crosses *G. hirsutum* × *G. barbadense*, but Harland did not find the hybrids up to the mark. Hutchinson (1937) points out that " specific differences result not from differences in any particular factors but from differences in average gene content and that the latter must be in dynamic and not in static equilibrium. The individual genes drift into or out of species according to their selective value relative to the genotype as a whole and to their mutation pressure."

POJ. POJ. 213 × Bamboo POJ 213.

(*With the kind permission of India Government from Ind. Jl. Agri. Sc.*)

Fig. 129. POJ. 213 Sugarcane and the hybrid with bamboo.

For a breeder, crosses between parents which do not largely differ in many of the major genes and also in which the modifier complexes in the two parents are not different and specific, selection from hybrid progenies may yield useful results. In the case of crosses between two true species or genera, the genetic

equilibrium is upset and hence the progenies show rapid break-down in the first few generations.

Interspecific crosses have been useful in the case of vegetatively propagated plants such as sugarcane. The first interspecific cross between *Saccharum officinarum* and *S. spontaneum* was effected by Barber in 1914 and also the intergeneric cross with *Narenga porphyrocoma* in 1916. Later, Venkatraman and Janaki have reported other intergeneric hybrids in sugarcane. The true species of *S. officinarum*, when used as female parent in the crosses did not

(*Photo from Sugarcane Expert.*)

Fig. 130. Bamboo and Sugarcane, which two were crossed at Coimbatore.

prove so successful as when the clone P.O.J. 2725 (2n–106) was used in the crosses with Sorghum as male parent. P.O.J. 213 and P.O.J. 2725 were used as female parents in a numbei of wide crosses. Table 88 shows some of the wide crosses attempted in sugarcane. (Figs. 127, 128, 129 and 130).

TABLE 88.

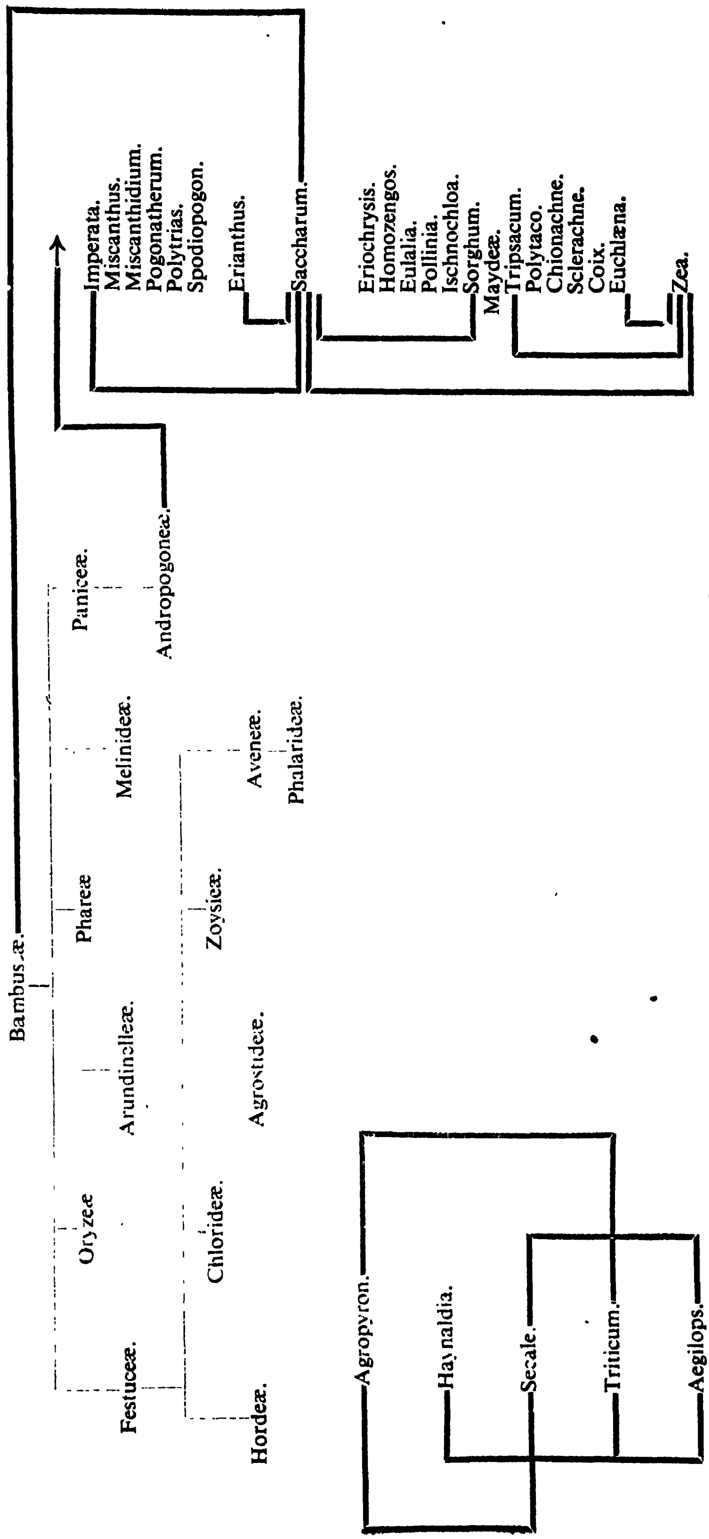
	II parent 2n.	F_1 2n.	Fertility of F_1.
I. *S. officinarum* 2n=80			
(1) Vellai × *Narenga narenga*	30	55	Sterile.
(2) E.K. 28 × *Erianthus sara*	60	60—70	Fertile.
(3) Vellai × *E. arundinaceus*	60	70	Sterile.
(4) Vellai × *Sorghum durra*	20	50, 90	Non-flowering.
(5) Vellai × *S. halepense*	40	60	Pollen sterile.
(6) Vellai × *Zea mays*	20 + 2*B*	52	Non-flowering.
II. *Saccharum spontaneum*—			
(7) Glagah 112 × *Erianthus ravennoe* ...	20	66	Fertile.
(8) Holes No. 1, 56 × *Sorghum durra* ...	20	38	Sterile.
(9) Coimbatore 64 × *S. durra*	20	...	Pollen sterile.
(10) Gigas, 124 × *S. durra*	20	...	„
(11) Gigas 124 × *S. halepense*	40	...	„
(12) Coimbatore 64 × *Bambusa arundinacea*	72	68	„
III. *S. officinarum* × *S. spontaneum and derivatives.*—			
(13) P.O.J. 2725 106 × *S. durra* ...	20	63—64 116—118	Pollen sterile.
(14) P.O.J. 2725 106 × *S. spontaneum* (*Holcus sorghum*).	20		
(15) P.O.J. 2725 106 × *Imperata cylindrica*....	20	120—134	Fertile.
(16) P.O.J. 2725 106 × *Bambusa arundinacea.*	72	90	Fertile.
(17) Kassoer 136 × *Sorghum durra* ...	20		
IV. *S. officinarum* × *S. barberi*—			
(18) P.O.J. 213, 124 × *Bambusa arundinacea.*	72	96—100	Fertile.

Sugarcane is a highly polyploid species and as such it easily crosses with distantly related genera. The crossability depends upon the degree of auto-syndesis in the parent. Some of the wide crosses attempted in sugarcane, wheat, and maize are diagrammatically shown in fig. 131.

S. officinarum is an octoploid (2n–80). The cultivated canes are divisible into two broad groups (i) Indian canes (ii) Noble or tropical canes. Their main characteristics correspond to the two wild races of canes *viz., S. spontaneum* and *S. robustum*, and probably the two groups of cultivated canes are derived from these two wild races. *S. spontaneum* has a wide range of distribution in South-East Asia, India, Burma, islands of Eastern Archipelago and New Guinea. *S. robustum* was recently collected in the islands of New Guinea. *S. spontaneum* is found wild in India (Fig. 132), and is polymorphic. In sugar content it shows variation from 0.5% to 17% and probably for this species India is a centre of origin.

Fig. 131. INTERGENERIC HYBRIDS

(modified from T. S. V. 1938, *Indian Science Congress.*)



Thick lines indicate the crossability between the genera.

(With the kind permission of India Government From Agri. Jl. Ind.)

Fig. 132. *Saccharum spontaneum* coming up as weed. This plant was utilised as a parent in the hybridisation work on *S. officinarum*. Some of the progenies were highly useful as improved Co. canes.

The commercial canes constitute complex interspecific hybrids between *S. officinarum* on one hand and *S. spontaneum*, *S. barberi* on the other. Inbreeding is not of any practical interest at present due to the fact that interspecific hybridisation yields quick results. However it was noted that results once attained by such crosses could not be repeated again due to the high variation and hybridity of the parents. Superior types could be evolved by complicated hybridisation between the thick canes and *S. spontaneum*.

The wide crosses in sugarcane were quoted to show that in the case of vegetatively propagated highly polyploid species like *Saccharum*, useful and quick results may be attained but such results in grain crops are more difficult to attain.

Recently, economically useful types have been selected from wheat-rye crosses. At one time wheat-rye crosses were not considered to be of value

Fig. 133. Hybridisation in tomato. (1) *Lycopersicum esculentum*, (2) *L. pimpinellifolium* (3) F_1 hybrid and (4) Back-cross.
(*With the kind permission of Ind. Jl. Gen. Pl. B.*)

but by persistent attempts winter hardiness was added to wheat. Interspecific crosses within the cultivated forms of New World and Old World cottons

have been attempted. Russians have selected useful types in the former but Harland does not find the cross useful in throwing types better than the parents.

In maize too, intergeneric crosses have been made. There are two species of *Euchlaena*—*E. mexicana* (teosinte) and *E. perennis.* Their chromosomes are partially homologous with those of maize. *Tripsacum* is much less related to maize and the cross maize × *Tripsacum* resembles the pollen parent while the cross *Tripsacum* × maize is not successful.

Fig. 134. *A disease resistant type selected from F_2 of the cross between L. esculentum and L. pimpinellifolium.*

In recent times, wide crosses have been attempted in vegetables. Much success has not followed these attempts. Crosses between the cultivated types and wild forms are useful in that certain " wild " characters, which are dominant, are absent in the cultivated forms. The wild forms possess many

characters of agricultural value, such as drought resistance, disease and pest resistance, hardiness, etc. Transference of these economic characters into the cultivated forms without in any way losing the existing useful characters is one sure way of improving the cultivated forms. The difficulty lies in the fact that the genetic balance of hybrid progenies is largely upset and stable combinations are difficult to attain.

In the case of tomato, economic types from interspecific cross *Lycopersicum esculentum* × *L. pimpinellifolium* have been selected at New Delhi. The fruits of *L. esculentum* are slightly flattened, corrugated and crack on opening. It is of acid taste. The plants are medium, early, and susceptible to common diseases. Yield is fairly good. *L. pimpinellifolium*, currant tomato, is a wild plant. It is characterised by small shining roundish fruits which do not crack on ripening and the fruits are borne in clusters. The plants are early and are resistant to many of the common diseases. In F_2 and subsequent generations of a cross between these two species, a number of plants with useful combinations were selected (Figs. 133 and 134).

7. Back-crossing.—The objects of back-crossing in plant breeding are (1) to reduce variation in further generations and (2) to increase the proportion of the genes of the recurrent parent in the progenies. In the case of intra-varietal crosses the variation in F_2 and later generations is not large and also the genetic balance is not broken down to any appreciable degree. In inter-specific and inter-generic crosses, the parents are comparatively genetically diverse and as such there is a general and rapid breakdown in the progenies and the selection of stable intermediate types of favourably recombined forms is difficult. A very large population must be raised if direct selection is to be adopted and the raising of such a large population is not possible for various practical considerations. Back-crossing helps in the reduction of genetic variability and by that the size of population may also be reduced.

In the case of inter-specific crosses the first generation hybrids may show sterility depending upon the degree of genetic relationship between the parents. By back-crossing, fertility may be increased. Harland in the case of cotton showed that transfer of individual genes is possible by repeated back-crossing. This author recommends back-crossing instead of searching in F_2, F_3, F_4, etc. families. He was able to transfer few genes from one species to another in the New World Cottons as shown in Table 89.

In the case of wide crosses, it is not possible to breed intermediate types without regaining the genetic balance of one of the parents (Hutchinson) and this is done by back-crossing. Skovsted recommends back crossing with the parent having larger number of chromosomes in the case of cotton, so that pairing between non-homologues may be maximum.

In *Triticum*, *Secale*, *Avena*, *Prunus*, *Zea*, *Nicotiana* back crossing have been attempted for selecting useful types.

8. Selection in hybrid progenies.—Most of the economic characters are quantitative and are governed by a large number of factors. The variation in respect of such a character shows a *mono-modal curve* in which the mean

TABLE 89.

Character.	Transferred from—to.	Remarks on new type.
Hairiness	*tomentosum to barbadense*	Intensely hairy with longish hairs.
Do.	*tomentosum to hirsutum*	Very hairy—short hairs.
White lint	Sea Island to Egyptian	Pale brown with longer lint than Egyptian.
Brown lint	Egyptian to *hirsutum*	Very pale brown lint.
Laciniated leaf	Upland to Sea Island	More laciniated and weak.
Long lint	Sea Island to Upland	Lint length reduced to 41 mm.
Naked seed	Upland to Sea Island	Practically lintless.
Red leaf	Upland to Sea Island	Red much weakened.
Crinkled	Sea island to upland	Less vigorous and productive.
Red leaf	Kidney tree to Sea Island	Little change.

is near to that of F_1 but the variability is far greater. If all the possible variations are to appear in the population of a breeder, the population must be very large and for this, each F_2 population must be sown covering some few acres. Harland (1934) in connection with the problem in cotton states " although fertile combinations of any two New World species are possible this is not the same thing as saying that the resulting combinations are of any value from the economic point of view. It is quite easy to say that *Gossypium tomentosum* is a xerophytic type habituated to an arid environment and poor soil and another thing to say that this valuable character can be incorporated into Upland or Sea Island cotton. The problem of transferring drought resistance from *G. tomentosum* to upland would be a task which a few years ago would be embarked on by the plant breeder in a light hearted optimism. Nowadays, we are by no means optimistic about the outcome of such experiments and we realise that much fundamental work in genetics has to be done before the possibilities of practical plant breeding can be stated. The ordinary method of plant breeding is to cross two species, grow a more or less big F_2, spend a lot of time in making frequency arrays of measurable characters which refuse to behave in rational mendelian manner, grow a lot of F_3 and F_4 families with the hope of finding desirable combinations and then either abandon the work or put something into cultivation which proves inferior after extensive practical tests. It is thought that by obtaining millions of plants in F_2, something valuable will turn up. So far as I know, the practical results of such work are very meagre and only in special cases where the species have been apparently closely related has any real advance been made."

In crosses between widely separated species, there is the mutual disintegration of genetic systems, which latter are co-ordinated in each species with environment. In F_2 segregation, mal-adjustments result. If the parents are closely related the degree of genetic breakdown is less. Largeness of the

number of factors that govern the character, *e.g.*, 200 to 300 factors possibly govern characters such as lint index, seed weight and lint length in cotton, and the possibility of breakdown in F_3, F_4 and later generations make it difficult for a breeder to confidently select the types in F_2.

Work of Mather (1941) on Drosophila is of interest in this connection. The character chosen by him for study is the number of chætæ on the ventral surfaces of fourth and fifth abdominal segments. The character is quantitative and also showed difference in the mean values of different species. Selection for increasing the chætæ was practised in two crosses and the results are discussed here.

In one cross where selection was exercised from F_2 onwards, the main advance was achieved in the first two selected generations and later selection was ineffective. In a second cross, selection was effective for two generations and this was followed by a period of stability. This was later followed by a second and larger advance with selection.

In nature in pure breeding plants, the genes are in a state of equilibrium or balance. On hybridisation, this balance is upset and variations are thrown out. The plants breed pure again when the genes regain their balance. In some cases, immediate genetic stability may be advantageous and in some others variation at a future generation may be advantageous due to a sudden change in the environment. Mather hypothesises that the stability or otherwise of the character is conditioned by two types of balancing (1) *Relational balancing* in heterozygotes and (2) *Internal balancing* in homozygotes.

It was further found that (1) selection affects all chromosomes and the balancing may stabilise or release variations from any one of the chromosomes of the complement. (2) recombinations in a small region of the chromosome may bring about large variations in the phenotype and (3) the + and — genes of different balanced combinations may recombine without releasing variations.

These provide mechanisms by which the population retains scope for releasing variations on which selection is effective.

The foregoing experiments are of interest to practical plant breeders inasmuch as they have a bearing on selection for improved characters in the hybrid progenies. Stable or nearly stable phenotypes store within them potentiality for throwing out variations based on different genetic constitutions. The breeder then faces the problem (1) in what generation of a cross, F_2, F_3 . . . . . F_n is selection to be made. If selection is to be effective, it must be made at a time when variation is at the maximum and the maximum variant must breed true in later generations. Mather's experiments show that in earlier generations, the variations are released by relational balancing and in later generations by internal balancing. (2) On the basis of phenotype an individual cannot be judged for its variability in future generations, as it can store small or large potentialities to change by balancing the + and — genes.

Linkage between factors restricts the possible number of recombinations appearing in F_2. Anderson (1939) pointed out that there are many genetic

causes for the restriction of free recombinations F_2 and he showed that in respect of two quantitative characters studied by him only 1/64 of possible recombinations appeared. His work is summarised here :

When two species A and B are crossed, the F_2 population reveals a large number of recombined types. Anderson (1939) studying the cross *N. alata* × *N. langsdorfii*, showed that these observed recombinations in F_2 "fall short of complete shuffling of the traits of the two species." This is diagrammatically represented in Fig. 135. It will be seen that the recombinations fall within a narrow ellipse connecting the two parents. The extreme recombinations in the left top or right bottom of the correlation chart (*F* and *G*) never appear even in very large F_2 populations. "There are in other words powerful restrictions to character recombination in the F_2." These restrictions may be due to—

(1) Gametic elimination.
(2) Zygotic elimination.
(3) Pleiotropy.
(4) Linkage.

Gametic elimination may arise due to chromosomal differences between the two parents. Pollen germination may be prevented due to various reasons chief of which may be mentioned the action of self-sterility genes.

Zygotic elimination may occur immediately after fertilisation by the failure of zygote to develop normally. The same may be brought about by the formation of immature seeds, loss of seeds in storage, failure of seeds to germinate, and the death of seedlings in early stages. Diseases and insects may eliminate some types in the field.

Pleiotropism.—If it is taken that a single gene is responsible for two characters X and Y, then changes in developmental processes of X will be correlated with those of Y ; *i.e.*, X is highly correlated with Y. In the cross studied by Anderson style length and tube length were highly positively correlated. It is not possible to break these combinations to secure recombination of the type short style and long tube or *vice versa*.

Linkage.—Recombinations between quantitative characters are severely restricted by linkage.

Anderson's experiment reveals that improvement in quantitative characters by selection of C in F_2 population of direct crosses is restricted in its scope (Fig. 135). By direct selection in F_2 the desired recombination cannot be achieved. The usual methods are (1) to self the F_2 and (2) to cross the selected F_2 with either of the parents.

A third alternative is suggested by the author : "*The most efficient crosses should be between the desirable combinations which are most like one of the parents in one of the characters with those which are most like the other parent in the other character*". It can be shown that the other intermediate types are extremely variable in their genotype and hence unreliable as parents. Therefore a cross between D and E in the diagram will give a high proportion of the desired recombination. Otherwise, this object could be achieved only by a lucky chance of selecting *C* in F_2.

This is an important point for selection of improved types in the hybrid progenies. By this method, the recombinations can be stepped up to the desired degree in the course of few generations by crossing between the suitable hybrid progenies.

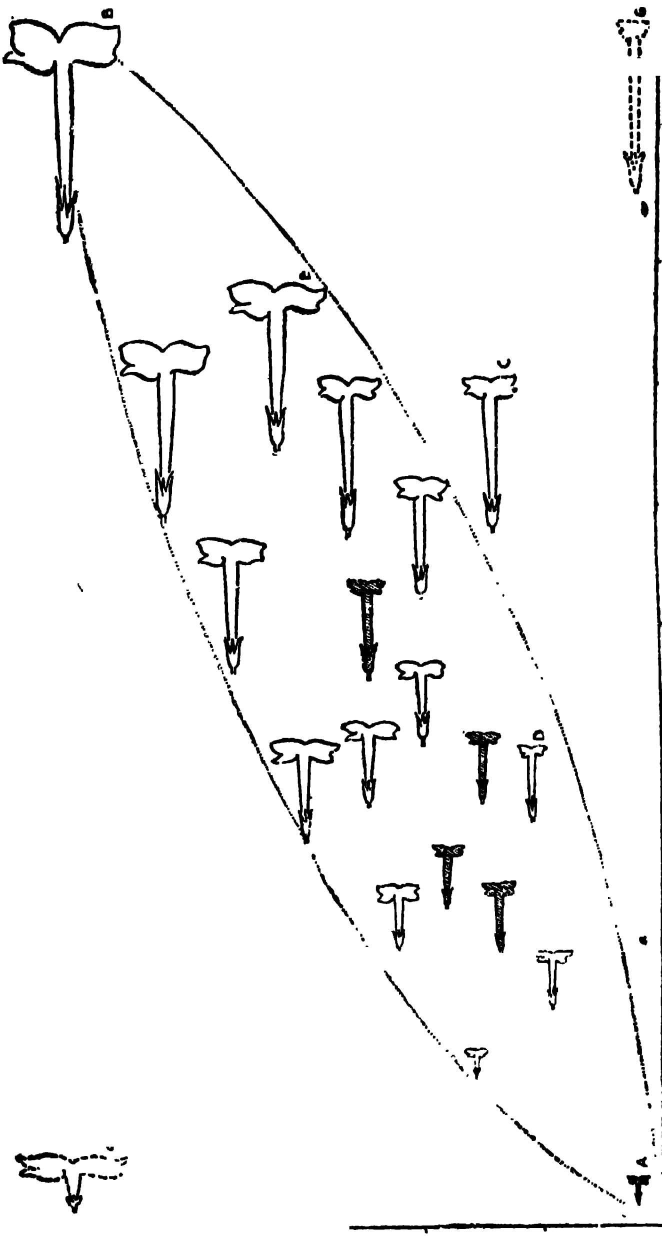


Fig. —iagram o explain Anderson's cross. The distribution of F variations is restricted to the area marked by elliptic. If the breeder aims to select a type approaching G nstead of selecting C and back-c ng to any the par nts, selection and inter-crossing of D and E are recomm ided.

The breeder relies on certain morphological characters in making selections in the hybrid progenies. Selection based on such characters as yield, tillering, etc., was not always successful. In rice, selection based on yield attributes such as tillering, ear formation, ear length, etc., gave indication of ultimate yield. Therefore, if all plants showing the model value in F_2 are carried

forward, useful selections could be made. In the case of cotton, yield attributes are complicated. In this crop, it is not only the yield but also the quality that is the ultimate criterion. Therefore, this method was not so successful in cotton.

Often it has been wished that if any simple qualitative character is found to be linked with the ultimate yield factors it will be helpful to the plant breeder. The qualitative character may be taken as the index for selecting progenies for their yield. An instance of this kind has been reported in *Sorghum*. In Milo × Kafir, the monogenic character, flat leaf was linked with quantitative economic characters like big panicle and thicker culms. Quantitative characters are governed by a large number of genes which are not all located in the same chromosome, but may be distributed in all the chromosomes. Therefore, there can possibly be no linkage between a qualitative and quantitative characters.

The breeder is left to rely on the ordinary methods of selecting types in F_2 and testing them in further generations for their usefulness. At present at the time of selection, the breeder is not sure of the stability of the characters for which he selected the particular individual. The problem is further complicated for the fact that most of the characters are affected to a larger or smaller measure by environment. Further, in the case of hybrids, heterosis enhances the expression of quantitative characters. Selection in the early generations of the hybrid progenies must take into account these two phenomena and proper field technique must be designed for the purpose. If heterosis is to be eliminated, the hybrid should be selfed for at least ten generations. This is not possible for a breeder because he has to wait for a long time before effecting selection ; secondly he will not have sufficient area to maintain all the hybrid progenies for so many generations ; thirdly, complete reduction to homozygosis may lead to poor vigour and yield ; fourthly, such a homozygote without scope for any genetic variability will prove a misfit under changing environment. The problem then is, in what generation the selection has to be started. At Coimbatore, in cotton, selection is made from F_2 onwards ; in rice selection is postponed to 5th or 6th generation ; in cholam it is done in F_2 generation ; in ground-nut it is done in F_2 generation ; in gingelly it is in F_2 generation or later. If selection is done artificially in the early generations when high degree of heterosis persists, it is difficult to judge the true survival value of observed characters. This brings us to the fact that sometimes the breeder may be selecting types that have no survival value and as such may not prove ultimately useful. In the case of Malwa and Nimar cottons, it was found by crop census that there are forces against narrow-yellow and broad-white. A study of unselected local bulk reveals the genotype or genotypes best suited to the tract.

Various methods of lay-out of plots in the field are adopted for eliminating the effects of environment. Fisher has suggested randomised blocks which are widely adopted. It has been pointed out recently by Hutchinson and Panse that complete randomisation of all the materials does not help in completely exhausting the variability of the selected types, *i.e.*, the technique is not fine enough and that the selected type may still be capable of further improve-

ment by re-selection. This was demonstrated to be the case in Malvi 9. According to their technique, the cultures belonging to a family are grouped together, a number of such families are first randomised and then within the family, the members are randomised. Analysis of the family totals shows the superiority or otherwise of the family and analysis of the individual members of the family shows whether there is still variability or not. This method of lay-out is termed " *compact family block* " and fuller details are discussed later.

Another important aspect of the problem of selection not only in the hybrids but also in pure lines from local bulks, is that selection must be carried out as far as possible in the tract for which the selection work is programmed. Environment has large-influence on the values of measurable characters and therefore selection made in one tract may not be suitable for another. The production of hybrid progenies may be done in any place according to convenience but the selection must be done in the agricultural tract concerned. This involves many practical considerations such as expenditure, staff and delimitations of the tract, etc., which we shall not discuss here.

In the case of commercial crops like cotton, establishment of numerous strains, each one suitable to a small area is not feasible for the reason that commercially the purity cannot be maintained for long in the various industrial processes. The seeds easily get mixed up at ginning centres and the seed purity is soon lost. This brings another problem to a breeder who is now made to select types that will come up well under a variety of agricultural and environmental conditions.

9. Limitation.—There are many limitations to hybridisation as a means for improving crops. In the case of crops which show wide variability in the local bulks, it is not necessary to attempt improvement by hybridisation. Straight selection in the local bulks may yield the desired results. Collection of types from other similar climatic and geographic regions may also be tried first. For example, in the case of rice and *G. arboreum* cottons, India shows centres of origin and therefore hybridisation without first exhausting selection in local bulks is not likely to yield quick results. There are attempts to introduce quality cottons, such as cambodias but these latter do not thrive under variety of conditions. Ayyar (1942) points out " the Russian expeditionists have reported that they came across in Mexico, Gautemala and Columbia numerous early and productive forms suitable to mountainous tracts, maritime low lands and sandy places, eco-types growing on the banks of rivers, lakes and also swamps. Harland and Kearney speak of the existence of valuable forms in S. America and around the gulf of California. Some of these types may be useful for the evolution of American forms which will be able to withstand the saturated soil conditions obtaining in the black soil during the early phases of plant development ". It may be pointed out here that the success of Russian breeders is mainly due to the collection of such valuable forms from the different centres of the world.

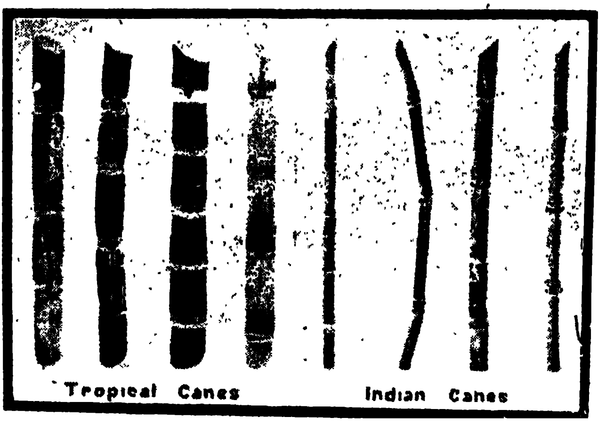
Another limitation to hybridisation is the difficulty in the choice of parents. Vavilov (1939) has instanced in the case of flax where the uneconomic type from Transcaucasia when used as parent increased the value of the best cultivated

type. It is difficult to have a complete picture of the genotype of the different species and races of the various cultivated types of crops and further, the interaction between different genotypes is another problem which require elaborate work for analysis. Therefore, at present choice of parents and selection in hybrids is " as much an art as science ". (Hutchinson 1936).

Crossability, incompatibility and cross-sterility are other limitations to hybridisation. The restriction in the number of possible recombinations that appear in F_2, limits the possibilities of success by hybridisation.

10. Achievements.—The plant breeding centres have achieved phenomenal success by selecting improved types in various crops. Though the plant breeder could not achieve what all he aimed at due to the limited knowledge available at present regarding the genetics of the crop he deals with, still, by hybridisation improved types have been built up. Hybridisation has been taken only as a method to increase the genetic variance of the population, where this was lacking in the local bulks. Lack of knowledge regarding the inheritance of the various economic characters and the genetic relationship between various races and species have made it impossible to plan hybridisation and selection. However with the recent advances in the genetic analyses of the crops general principles are being understood. Ramiah (1941) remarks that " such achievements have been brought about not with the definite knowledge of the inheritance of the particular characters whose combinations have formed the end in view. Can the geneticist suggest more rational methods of what to select and how to select in the hybrid progenies and give information on the genetic variance involved in the different generations starting from the F_2 ? "

As an example of success by hybridisation may be mentioned the work of Sir T. S. Venkatraman in Sugarcane. The Coimbatore seedling canes evolved by him are mainly responsible for the improvement in the sugar industry of this country. (Figs. 136 & 137). This was achieved by the '*nobili-*

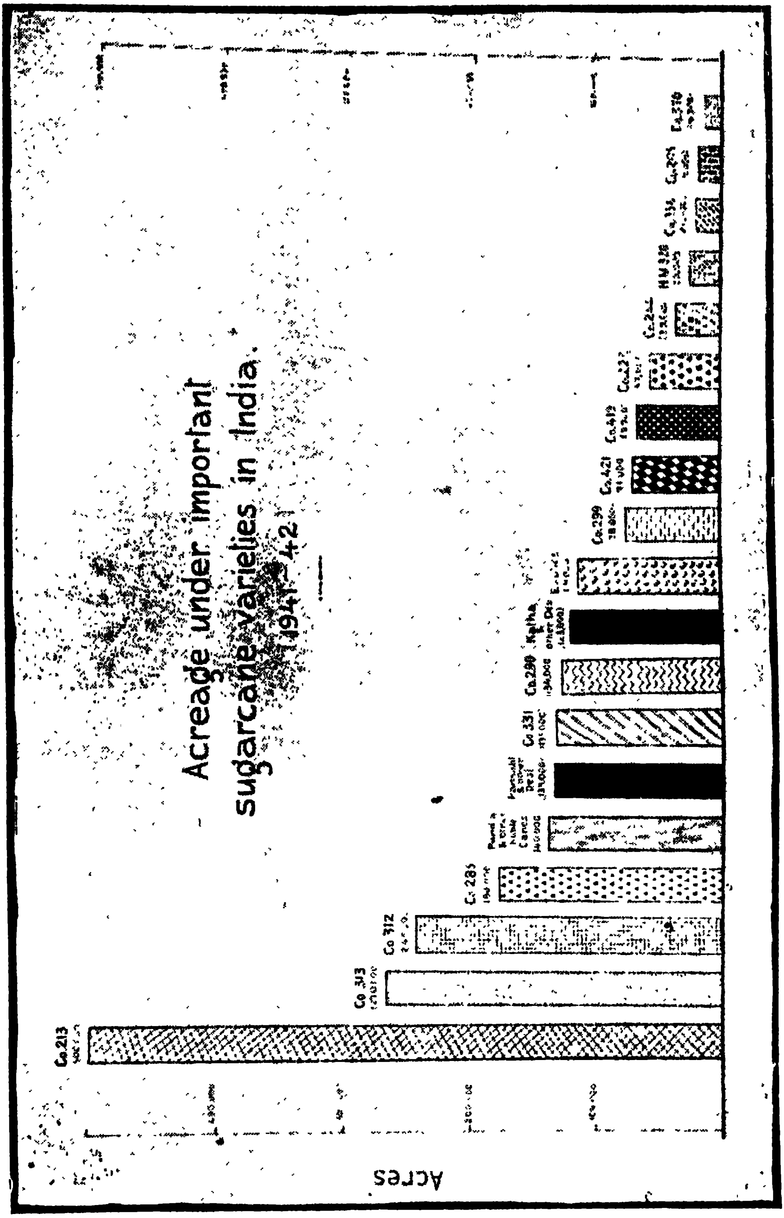


(*Photo from Sugarcane Expert.*)

Fig. 136. The poor indigenous canes of India and the thick canes.

sation' of the Indian canes. (Fig. 138). The Coimbatore canes not only occupied 75% of the total area but also was found suitable in other countries. The world distribution of Coimbatore seedling canes is shown in Fig. 139.

Recently intergeneric crosses have been made in this crop and especially sugarcane × *Sorghum* crosses have shown the possibility of reducing duration considerably.

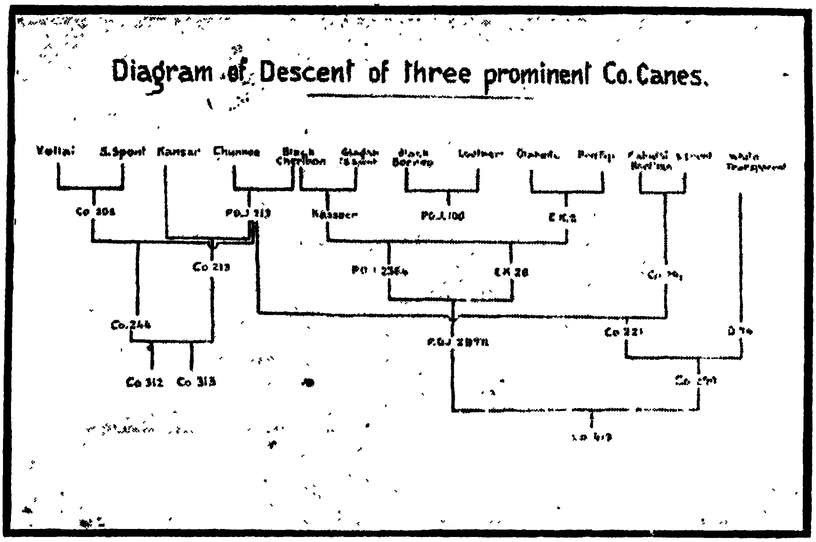


(Photo from Sugarcane Expert.)

Fig. 137. Important Sugarcane varieties of Coimbatore and the area under cultivation.

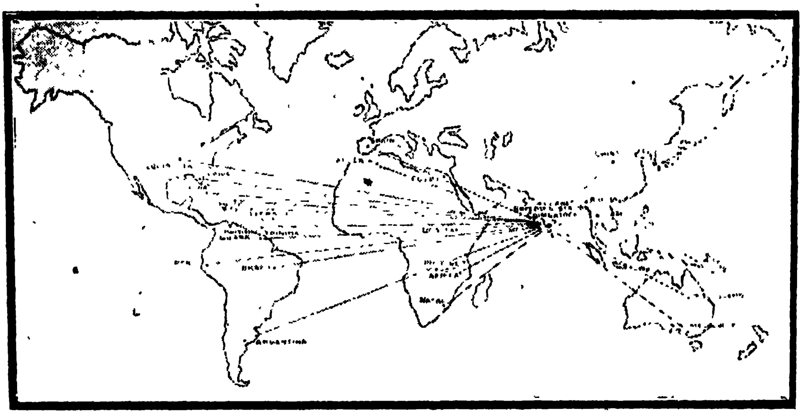
In rice, new types have been evolved combining yield and strength of straw, yield and resistance to paddy-blast, yield and shorter duration. In cotton,

yield and quality of lint have been combined. The following are some of the strains evolved by the breeding stations in Madras :



(*From Sugarcane Expert.*)

Fig. 138. Descent of Co. 312, Co. 313 and Co. 419 seedling canes of Coimbatore.



(*Photo from Sugarcane Expert.*)

Fig. 139. Countries to which Coimbatore canes have spread.

RICE—(*Oryza Sativa.*)

COIMBATORE STATION.—

Co. 1 ... Isolated from a natural cross in G. E. B. 24. It yields 20% over G. E. B. 24. Its rice is coarse and it is later by a week in duration. Grain size : $8{\cdot}5 \times 2{\cdot}6 \times 1{\cdot}6$ mm.

Co. 14 ... Hybrid progeny of a cross *Co.* 3 and a Burma variety with bunched earhead and stiff straw. It combines the grain quality of *Co.* 3 and straw quality of Burma rice. It yields 10% over *Co.* 3.

Yield per acre : 3,000—4,000 lbs.
Grain size : 8·6 × 2·6 × 2·0 mm.
Glume colour : Straw.

Co. 15 ... Isolated from a cross between G. E. B. 24 (resistant to paddy blast) and Korangu samba of Tanjore (highly susceptible to blast). It yields 15% over the local bulk. It may go up to 50% over the local in years of severe out-break of the disease.
Grain size : 7·7 × 2·9 × 2·0 mm.
Glume colour : Dirty in furrows.

Co. 16 ... Hybrid progeny of a cross between G. E. B. 24 and Korangu samba as noted above. It is non-shedding. It yields 15—20% over local bulk. Its grain is coarse.
Grain size : 8·1 × 3·1 × 2·0 mm.
Glume colour : Dirty in furrows.

MARUTERU STATION.—

Mtu. 15 ... Hybrid progeny of a cross between Garika Sannavari and Nallaru. Unlike Nallaru, it stands early planting and combines all good qualities of the other parent. Less shedding and non-lodging ; yields 5—29% over Mtu. 9.
Grain size : 8·3 × 2·5 × 1·9 mm.
Glume colour : Straw.

Mtu. 16 ... Isolated from a natural cross between local Konamani and a floating type from Burma. Characterised by tall growth with thick straw, non-lodging and capacity to withstand submersion. It is recommended to low lying lands. It is a coarse grained type.
Grain size : 8·5 × 2·8 × 2·0 mm.
Glume colour : Straw colours with purple tip.

COIMBATORE STATION.—

Co. 3 ... Progeny from the cross *Co.* 2 × *N*4 (African type). It yields 300 lbs. lint under irrigation and 125 lbs. lint under rainfed condition, per acre. Its ginning percentage varies from 38—34—30 under different conditions. Staple length 1″—1-1/16″. It is early and jassid resistant. It spins upto 50's. It is a quality cotton.

Co. 4 ... It is a progeny from the cross A. 12 × *Co.* 2. It yields 300 lbs. lint per acre under irrigation and 125 lbs. lint under dry rainfed conditions. Its ginning percentage ranges from 34—30. Staple length 1″ - 1-1/16 in. It spins upto 43's. It is very early jassid resistant quality cotton.

4463 ... It is a progeny of *Co.* 2 × *N*4 (African type). It yields 300 lbs. lint under irrigation and 125 lbs. under rainfed conditions. Ginning percentage 35. Staple length ⅞″—1″. It spins upto 42's. It is very early, suited to early sowings.

Co. 5 ... Selection from the hybrid between *G. Arboreum Var neglectum, forma indica* and *forma assamica*. It yields 105 lbs. lint per acre under rainfed conditions. Ginning percentage 32. Staple length ⅞″—15/16″. It spins up to 30's. It is a quality cotton.

GUNTUR STATION.—

X. 20 ... An inter strain cross between 171 and 45. It yields 60 lbs. lint per acre. Ginning percentage 28. Staple length ⅞″. It spins upto 32's. It is earlier and better than Cocanada's.

Chapter 20

BREEDING FOR DISEASE AND INSECT RESISTANCE

IMPORTANCE OF THE PROBLEM—NATURE OF DISEASE RESISTANCE —RESISTANCE DUE TO MORPHOLOGICAL FACTORS—PROTOPLASMIC RESISTANCE—ACQUIRED IMMUNITY—PHYSIOLOGICAL FORMS —INHERITANCE OF DISEASE RESISTANCE—BREEDING FOR DISEASE RESISTANCE—ACHIEVEMENTS

1. Importance of the problem.—Loss due to pests and diseases is enormous every year. " Prevention is better than cure " is amply true in the case of crops also. When once a crop suffers from damage by pests or diseases, the control measures may be costly and not economic. This is especially so in India where the holdings are generally small and it is not within the means of the cultivator to adopt the elaborate processes of control as practised in the West. The high cost of imported chemicals and machinery is a serious point for consideration by a small cultivator. Leaving apart the methods which involve elaborate machinery and chemicals for controlling pests and diseases, the only methods that are within the reach of ordinary Indian cultivators, are clean cultivation, rotation, sowing disease free seeds and the strict enforcement of Pest Acts wherever practicable. Therefore raising of improved types of crop plants resistant to pests and diseases is the cheapest way of solving the problem without embarrassing the cultivator. The extent of damage done by pests and diseases is not fully realised in this country. The data in Table 90 indicate the loss due to insects alone in U.S.A.

TABLE 90.

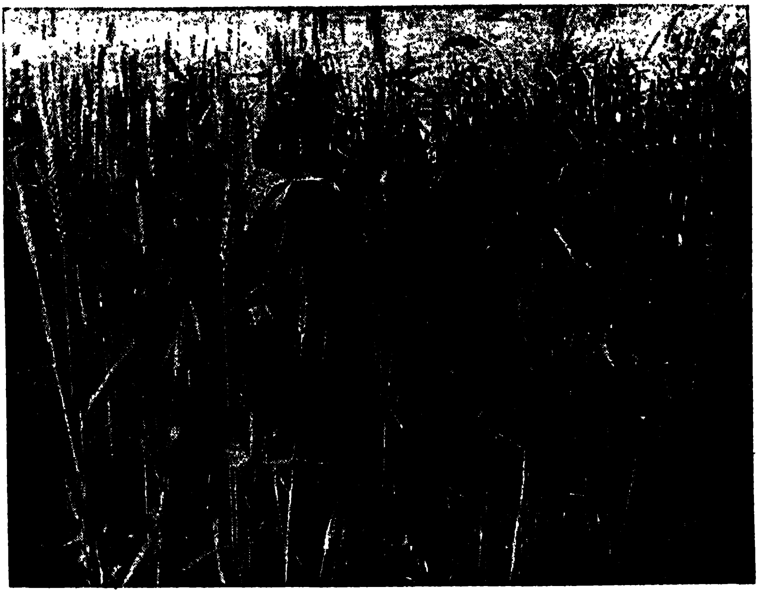
		$
Total	estimated damage to staple crops ...	8,29,419,900
„	to vegetables	64,894,000
„	Fruit crops	42,504,400
„	to nursery and greenhouse ...	7,737,200
„	to Livestock	140,389,000
„	to Storage products	300,000,000
„	to forest products	130,000,000
„	by carrying human diseases ...	75,100,000
	Grand Total ...	1,590,044,500

Loss of crops due to fungus and bacterial diseases is much greater than this. The annual loss in respect of 7 crops estimated in U.S.A. is shown in Table 91.

TABLE 91.

	Range	Average loss
Wheat ...	8·9—17·0	10·8
Rye ...	1·4— 2·3	1·9
Oats ...	4·8—6·8	6·4
Barley ...	3·8—11·2	5·0
Corn ...	6·0—10·7	8·0
Potatoes ...	16·2—21·7	19·6

Normally it may be estimated that on average every crop suffers at least 10% damage by diseases. In seasons of severe infestation of any one particular disease, the crop may be lost in entirety or may easily suffer 50% damage (Fig. 140). The farmer's margin of profit is generally small enough and



(*With the kind permission of Proc. Ind. Acad. Sc.*)

Fig. 140. A variety of wheat highly resistant to loose smut growing side by side with highly susceptible one. Both were artificially infected.
Note:—The severe loss due to the disease.

especially so in this country and any extra expenditure to be incurred by him in controlling pests and diseases is a big slice in this margin. Co. 213, an improved type of sugarcane went out of cultivation in United Provinces and Bihar due to severe damage by red rot. *Piricularia* causes serious damage to the rice crop in Tanjore delta. Therefore, the most economic proposition is to breed strains immune or resistant to most common diseases and pests.

The nature of damage by insects and fungi are varied. The possible causes that enhance or minimise this loss are also complex. The following are some types of damages caused by insects :

(1) by chewing stems, leaves, flowers and fruits of crop plants.

(2) by sucking the sap of plants.

(3) by boring tunnels into stems, the whole plant may dry up ; or by tunneling into fruits, etc., they may cause damage to the products.

(4) by attacking underground portions the aerial portions may dry off. In the case of root crops, the damage may be directly to the produce.

(5) by cutting or tunneling into plant parts nests are prepared by insects.

(6) in some cases, the insects may act as carriers of virus diseases from one plant to another or from one field to another.

Similarly the damages caused by fungi are manifold. Some of them are indicated below :

(1) The fungi may kill the entire plant, *e.g.*, wilt in cotton or red gram ; the death may occur even in the seedling stage as in the case of '*damping off*.'

(2) The entire organ may be killed while the rest of the plant may not be seriously damaged, *e.g.*, smut in cholam.

(3) Spots may be caused in stems and leaves, *e.g.*, rust in wheat, leaf spot in groundnut.

(4) The disease may cause proliferations, *e.g.*, green ear disease of cumbu.

(5) The disease may cause rotting, *e.g.*, bud rot of palmyra and coconut ; Mahali of arecanut.

Each type of pest or the organism causing disease has its own optimum set of conditions that favour their rapid growth and maximum damage to the crop. In nature, temperature, rainfall, humidity, etc., are some of the factors that affect the spread of disease.

For a breeder, the term 'disease' implies any abnormality caused by an upset in the normal functioning of physiological system of the plant. In this text, the term disease will be used in that broad sense.

2. Nature of disease resistance.—*When a particular individual plant or group of plants does not show the pest or fungus attack, it is important to know whether this is due to real immunity or to any other temporary causes that might have made infection difficult* ; or in the particular case the plants may merely *escape* and be free of the disease because by chance there was no infection. In the case of certain diseases and pests which are seasonal in their appearance, the plants may escape infection by finishing the life cycle earlier, *e.g.*, late sowing of cotton in S. India reduces attack by *Pempherulus affinis*, the cotton stem weevil. Similarly, it is reported that in Java, *Tephrosia* proved resistant to *Platysomid* beetle by the seeds hardening earlier and thus preventing the beetle from laying eggs on them.

There are various factors which affect both the host plant and the pathogen and the reactions between the two, and as a result the plant may become diseased or prove resistant. When artificially inoculated, all the plants may take the first infection. *The immune types of plants resist further growth and spread of the pathogen whereas in the susceptible types the pathogens spread rapidly.* The external conditions such as soil, water, climate, manure, etc., and the internal chemico-physical-physiological conditions of protoplasm decide the reactions of the host plant to the pathogens. Similarly the meteo-

rological conditions, and the reactions of the host plant decide the extent of spread of the pathogen in the host. *Even if the plant is of susceptible type, the life cycles of the host and parasite may fall in different seasons of the year and thus the pathogen may not meet with ideal conditions for invading the host and the latter thus escapes the disease as already pointed out.* Therefore to identify a truly immune type, all factors relating to both the host and pathogen are to be considered and the plant breeder should not judge the plant as immune merely because it is disease free at the time he observes it.

Leaving apart the cases of escapes, disease resistance may be classified as partial or complete. The latter is termed *immunity*. The nature of resistance or immunity depends upon the mode of attack. Taking only the fungi, *resistance may be protoplasmic or morphological. Stakman showed that resistance is often due to physiologic incompatibility between the host and the parasite and in such cases the invading pathogen sets up a reaction in the invaded cells even at the initial stages and as a result, the few invaded cells and the invading fungi may die due to toxic substances on one hand and want of nourishment on the other.*

The disease causing organisms choose the proper host that satisfies them and thus they show remarkable selectivity. In the case of white ants, which cause serious damage to cotton crop in Sind, the attack is very severe on Egyptian types as shown in Table 92.

TABLE 92.

PERCENTAGE OF PLANTS ATTACKED.

Egyptian types.		American types.			Desi.
Boss III	Ashmouni	4*F*	285*F*	289*F*	27 *WN*
90	86	55	49	56	32

In the case of Sorghum stem borers it is reported that the attack is always more in the case of sugary varieties.

In *Sorghum*-Sugarcane hybrids aphids were found to attack the hybrids only or the *Sorghum* parent and not the sugarcane. This shows the capacity of the insect to differentiate and identify the proper host.

3. Resistance due to morphological factors.—*In the second type of resistance the plant may present certain morphological features which may make it difficult for the attacking organisms to cause any damage.* In the case of stem rust in wheat, mycelium develops in collenchyma only, and in the case of varieties with reduced layers of collenchyma and larger sclerenchyma, rust development is poor. These varieties are susceptible at seedling stage but they become resistant when sclerenchyma are fully developed. Similarly, in the case of Jassid resistance in cotton it is generally noticed that hairy types are resistant to the pest, though there are varieties like 43F of the Punjab which are hairy and susceptible.

Development of mechanical tissues that are hard for penetration by the fungi or insect is a common feature met with in resistant types. In the case of flax wilt, caused by *Fusarium lini*, the pathogen penetrates the plant through root hairs, young epidermal cells, stomata of seedlings and perhaps through wounds. Clogging of vessels is not considerable. Wilting may result from (i) destruction of young active root system, (ii) diversion of nutrients to the fungus and starvation of host, (iii) vigorous growth of fungus increasing the transpiration of the host, (iv) possible production of toxins by the fungus. In resistant varieties, the fungus stimulates the formation of cork cells adjacent to the region of penetration and hence it is not able to penetrate to considerable extent. The failure of fungus to penetrate may be due to the formation of cork and probably also to protoplasmic resistance. The degree of resistance by a strain is largely variable due to environmental conditions under which the plant grows.

In cotton wilt, the fungus enters the roots by mechanical means. In the susceptible types the fungus penetrates layer after layer and reaches the xylem on the 8th day. In the resistant types the fungus could reach one or two outer layers only because rapid penetration by the fungus is retarded by cork formation. A similar instance is noticed in the case of wilt in Bengal gram (*Cicer arietinum*). Resistant types showed thick layer of suberin in root sections and this is lacking in susceptible types. The rate of development of fungus is also low indicating that resistance is of both morphological and protoplasmic type.

Similar resistance to insect attack is also known. The most common species of cut worm in N. India are: *Agrotis ypsilon A. nigrum*, *Euxoa spinifera* and *E. segetum*. In the case of severely attacked gram, stem diameter is small and secondary wood weakly developed. In the types which are slightly attacked, the stem diameter is large and secondary wood well developed. Moderately attacked group is intermediate in structure. The average diameter of stem in the three groups is shown in Table 93.

TABLE 93.

Group 'A' very slightly attacked.		Group 'B' moderately attacked.		Group 'C' severely attacked.	
Variety.	Average diameter mm.	Variety.	Average diameter mm.	Variety.	Average diameter mm.
3	2·45	9*	1·58	17	1·58
26	2·76	36	2·20	46	1·58
38	2·82	41	1·83	52	1·46
79	2·79	58	1·92	82	1·52

* Later included in group 'C'.

Environment has large influence over the development of wood. At Karnal the development was vigorous and hence cut worm attack was slight.

Red-rot in sugarcane is caused by the fungus *Colletotrichum falcatum.* The fungus enters the plant through wounds. It enters the vascular bundles and travels up along the xylem vessels ; lateral spread in the stem is effected by the fungus piercing the vascular sheath and spreading in the parenchymatous ground tissue. Anatomical features of the resistant and susceptible canes showed that resistance increases with (1) increased sclerenchyma

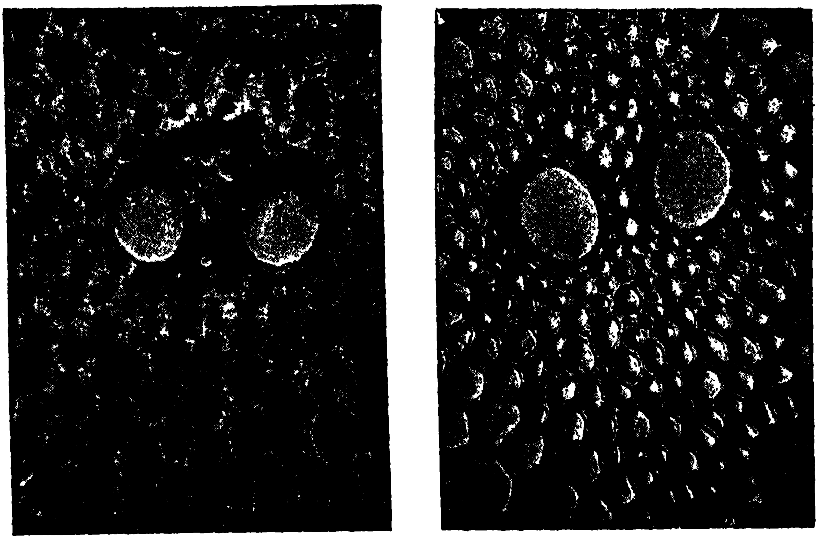
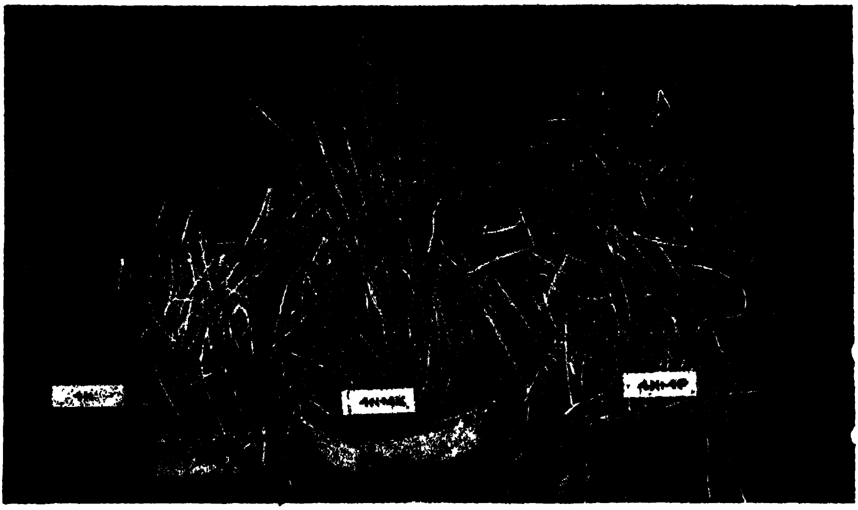


Fig. 141. Sclerenchyma round the Vascular bundles in Sugar-cane (left), Resistant type (right) susceptible type. (*After Kedarnath*).

thickening round vascular bundles ; and (2) fewer number of continuous xylem vessels. Red-rot resistant sugarcane varieties and the wild allies like *S. spontaneum* and *Sclerostachya* show highly lignified vascular sheath and very few continuous xylem vessels. (Fig. 141).

Reference was already made to jassid resistance in cotton where types with plant body hairiness resist the pest much more than the glabrous ones. In the case of fungi penetrating the host plant through stomata, the size of the latter is a factor of resistance.

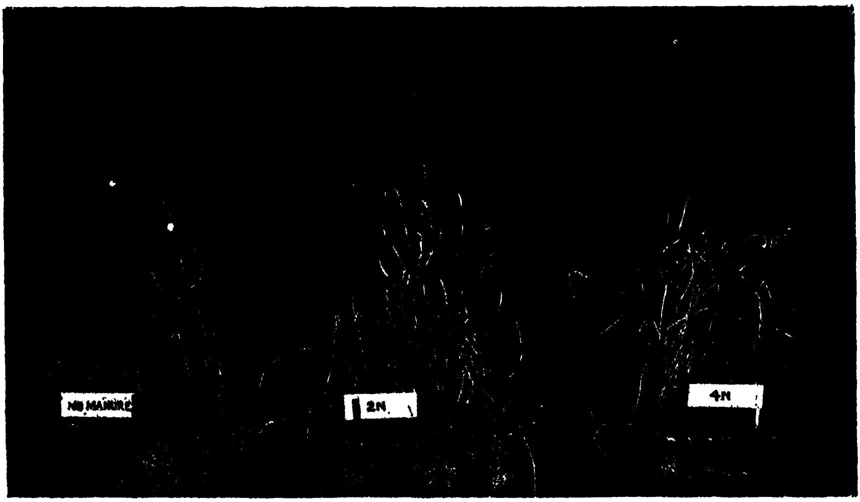
4. Protoplasmic Resistance.—Apart from the genetic constitution and the morphology, the internal condition of the plant affects the extent of resistance to disease. Red-gram wilt caused by *Fusarium vasinfectum* varied with manurial treatment. Superphosphate or farm yard manure increased it while green manuring with sunn-hemp reduced it. In rice, resistance to *Piricularia* varied with the manurial treatments. (Figs. 142 and 143).



(*With the kind permission of M. A. J.*)

Fig. 142. The effect of manures on the susceptibility of *Korangusamba* to *Piricularia.* Note that increasing doses of nitrogen increase susceptibility.

Vigour of the plant is a factor for resistance. Vigour is governed by soil fertility, aeration, manurial treatments and climate. Vigorous growth may confer power of recuperation from the attack and thus reduce the damage. In the case of corn root worm, the ability of the plant to recover from the attack is an important factor. Irrigation is an important item in this connection. Insufficient water supply is found to weaken the plant and increase



(*With the kind permission of M. A. J.*).

Fig. 143. The effect of manures on the susceptibility of *Korangusamba* to *Piricularia.* Note that the withering of leaves is greater with increasing doses of nitrogenous manures.

susceptibility as in the case of cotton and sugarcane to sap feeding insects. In cotton, irrigated varieties are more susceptible to *Pempheres* damage.

Increased ash content in wheat was found to enhance resistance to Hessian fly. An increase in the ratio of potash to phosphoric acid in tea leaves diminishes its susceptibility to *Helopeltis*. When cotton plants are treated with sodium selenate, aphis breeding is inhibited and adult mortality is caused. In such treated plants, adult mortality of pink boll worm is noticed. Application of ammonium sulphate to soil reduces plant susceptibility to root knot eel worm. The degree of resistance may change when the plants are taken to new locality. At Koilpatti area and Nizam's dominions, *Pempheres* on cotton is absent due to high temperature prevailing in the tracts. Hybrid corn resistant to corn borer in Michigan lost its resistance and was susceptible when grown in Ohio. In the case of mosaic disease of sugarcane geographical variation in resistant types is noticed. Co. 290 is resistant to mosaic in North India and certain other countries while at Coimbatore it shows 70% infection.

The betel vine disease in Noyel valley which was investigated was found to be due to soil conditions. Water content of the soil affected the crop in its mineral composition as pointed out in Table 94.

TABLE 94.

	Healthy %	Diseased %
$Fe_2O_3 + Al_2O_3$	0·66	0·44
CaO	1·82	2·02
MgO	1·32	1·79
K_2O	5·13	3·83
P_2O_5	0·66	0·55

The investigations on leaf roll and red leaf of cotton showed that the death rate of roots in diseased plants in upper layers of soil was too high for formation of new roots to compensate. Total active root length in lower zone was less. Balance of growth in plant is upset as revealed by lower concentration of sap and N-content of leaves. Soil deterioration during the crop season is the main cause of the disease.

Onion smudge is caused by *Colletotrichum circinans*. White variety of onions is highly susceptible while the yellow and red varieties are not. Biochemical studies showed that protocatechuic acid which is present in the outer scales of the resistant varieties is responsible for the resistance. Tannin occurs along with this substance and tannins are widely distributed in the plants. It is not definitely known whether it plays any part in disease resistance. In the case of flax wilt, it was found that a substance, suspected to be of the nature of a glucoside is present in extract of resistant plants. This principle inhibits the growth of the fungus. In *Helianthus annuus*. *Artemesia* and *Xanthium*, peroxidase was related to resistance to rust. It was lowest in immune plants. A substance that inhibits the action of enzymes of the fungi was found to be correlated with the disease resistance.

5. Acquired Immunity.—Animals can resist diseases by acquired immunity. They produce certain antibodies which enable them to resist future attacks. In the case of human and cattle epidemics, inoculation of serum and vaccine is a valuable step in inducing immunity and controlling the epidemic. It will be of practical interest to know whether such acquired immunity is possible in plants.

The plants differ from animals in their circulatory system and growth. The circulatory system of animals is rapid and efficient. Every tissue is well served by capillaries and the blood reaches even the remotest cell in comparatively a short period. This rapid circulation of the body fluid is responsible for the quick transport of antibodies to every organ of the animal. In the case of plants, xylem and phloem are the main channels for the transport of body fluids. The flow of liquid in them is very slow. Further, they are comparatively effective so far as the vertical flow is concerned, but for lateral spread of the fluid they are very ineffective. Thus it may be said that the circulatory system in plant is not well adapted for the efficient spread of antibodies as is the case in animals.

In the manner of their growth, plants differ very much from animals. The latter have definite growth, and during their growing period, every organ and part of the body grows proportionately. In the case of plants, there are many growing points (such as apical meristems and axillary buds) and fresh tissues are laid in an indeterminate fashion. The growth progresses season after season and may not cease. This sort of growth is not conducive to the spread of the antibodies. Even if it spreads, the increase in plant body size year after year may dilute the antibodies to an ineffective low concentration.

Several investigations point to the fact that there is acquired immunity in plants. First, tests were conducted in 1901 by Ray and Boverie. Several investigations have been carried out since then. No satisfactory technique has yet been found to make artificially induced phyto-immunity an effective tool to prevent diseases in plants.

6. Physiological forms.—Both in insects and fungi attacking the plants there are physiologic forms. Just as there are varieties in crop plants suited to different ecological conditions like drought, salinity, ill-drained soils, flooded areas, etc., there are different strains of insects and fungi. There are no morphological differences between the physiological forms but they differ in their pathogenicity. Taking rust of wheat as example, it has been found that the pathogen *Puccinia graminis tritici* exists in no less than 50 physiologic forms. These physiologic forms are distinguished by their culture characteristics and choice in attacking twelve standard wheat varieties. Similarly, three physiologic forms have been recognised in the case of *Sorghum* smut, *Sphacelotheca sorghii* ; in the case of stem rust of oats there are six physiologic forms.

The work done on cotton wilt may be mentioned here as an example. Gadag I is a selection from American cottons introduced into India over 100 years ago. Gadag I and other recent introductions like Cleveland-big-boll,

Dixie triumph, Sea-Island and others are immune to wilt under Indian conditions. The immunity is evidenced even when the American strain of the fungus is used for infecting under Indian conditions. The Indian fungus was tested against the local and American cottons under American soil and the data are presented in Table 95.

TABLE 95.

Cotton Variety.	Fungus strain.	Total No. of plants.	No . of wilted plants.
Indian (Dharwar I) ...	Indian	28	6
Indo-American (Gadag I).	„	32	0
Indian (Dharwar I) ...	American	28	0
Indo-American (Gadag I).	„	28	23
Indian (Dharwar I) ...	„	23	0

The data show that the Indian fungus is slightly pathogenic to Indian cottons under American soil conditions but it is not pathogenic to foreign or acclimatised American types. Similarly, the American fungus is not pathogenic to Indian cottons. The Egyptian form of *F. vasinfectum* is mildly pathogenic to both Indian and American cottons.

Physiologic forms in the case of insect pests also are present. In respect of cotton stem weevil, *Pempherulus affinis* which is a serious pest on the cotton crop in some districts of Madras Presidency, it was found that the same insect is also present in the hills far from any cotton crop and in such cases the pest attacks *Triumfetta rhomboidea.* " Certain behaviouristic differences between the two populations have also been noted, although no morphological differences are to be found. The mode of attack in the two hosts, the parts attacked and the density of population supported by them show significant deviations. The observations recorded above are however strongly suggestive of the possibility of the species having different strains." (Krishna Ayyar 1938).

In the case of fungi, the physiologic forms may be distinguished by the following methods :

(1) by their reaction on selected host plants.

(2) cultural characters as exhibited by the pathogens when grown in culture media.

(3) physico-chemical reactions.

In respect of insect pests, tests may be conducted to find out differences in the choice of host plants, changes in life cycle, associated parasites, etc.

Physiologic forms are definite, genetic entities. Any new variation in pure-line cultures of crop plants can arise by mutation or hybridisation with other types.

Similarly, in the case of physiologic forms of fungi or insects, any change in their culture characteristics can arise by gene mutation or hybridisation with other forms.

7. Inheritance of disease resistance.—Many crop plants such as maize, tobacco, sugarcane, etc., are found under cultivation only and they are never truly wild. These crop plants require not only careful cultivation but also they require protection from pests and diseases. In the course of their evolution they have lost certain of their characteristics which were useful to their progenitors in their wild state in resisting pests and diseases.

It is therefore evident, that resistance to pests and diseases has played an important role in the survival of the fittest and like many other morphological characters, is inherited and is subject to Mendelian laws of inheritance. It has already been pointed out that even the physiologic forms of fungi and insects are definite genetic entities.

On one hand, resistance to disease by the crop plants is a genetic character and on the other, the degree of pathogenesis by insects or fungi is also a genetic character. It is therefore possible to breed varieties of crops resistant to any particular disease. In this connection, there are two aspects of the problem which require our consideration : *viz.*, (1) whether by constant contact with the pathogens, the plant develops immunity, (2) whether the plant loses such immunity by being out of contact with the pathogen for long periods. These two aspects were studied by Barker in the case of wilt resistance in flax. He found that some varieties contained genotypes for resistance while others had none and that the susceptible types did not develop resistance by virtue of contact with the pathogen nor did the resistant type become susceptible because of its being raised under disease free conditions. American cottons are susceptible to American form of *Fusarium* and resistant to Indian form in spite of more than 100 years' isolation from the former and contact with the latter for that period. These indicate that immunity or susceptibility is a genetically controlled character. The pests or pathogens, may develop new strains that begin to attack the variety of the crop plant that once proved resistant. This raised doubt in the minds of the plant breeders as to the utility of breeding for disease resistance.

Fusaria are facultative parasites and are specialised in their parasitic relations. Breeding for resistant types is the common method for controlling the disease. In the study of such genetic characters, the following should be borne in mind : the genetic basis of inheritance, the relation of environment to the expression of resistance, the activity of the parasite, the relationship between parasite and host tissue and the genetic variability of the host and pathogen.

The number of genetic factors controlling disease resistance varies in different plants. In the case of wilt disease of tobacco, tomato, flax and cotton, a complex genetic basis is evident. In the case of pea, resistance is monogenic dominant to susceptibility. In cabbage, it may be due to a single gene (type A) or may be complex (type B). In both the types of resistance, the host-parasite relation is alike but type B resists parasites at lower temperatures only. In the

TABLE 96.

Variety.	Parental value.	% of mortality.																	Total.
		0	5	10	15	20	25	30	35	40	45	50	55	60	65	70	75	80	
Strain 468 (resistant type) ...	...	16	23	18	5	2	...	...	...	...	..	...	...	...	...	...	...	...	64 samples.
Strain 19 (susceptible parent) ...	...	...	...	...	...	7	12	11	11	8	5	4	4	2	...	...	...	1	64 ,,
F_2 (classified from F_3 behaviour) from healthy plants.	...	9	10	5	5	5	4	4	3	4	...	...	1	...	...	...	...	...	50 families.
F_2 (classified from F_3 behaviour) from healthy wilted plants.	...	...	...	1	...	...	...	...	...	...	...	...	1	1	...	2	2	2	9 ,,
F_4	0%	15	9	2	...	...	...	...	...	...	...	...	...	...	...	...	...	...	26 sibs.
	3%	20	22	16	...	...	...	...	...	...	...	...	...	...	...	...	...	...	58 ,,
	9%	11	13	2	...	...	...	...	...	...	...	...	...	...	...	...	...	...	26 ,,
	26%	...	1	3	2	2	3	2	...	...	...	...	...	...	...	...	...	...	13 ,,
	77%	...	...	...	...	2	1	3	3	3	3	1	6	3	...	...	...	...	25 ,,
	77%	...	...	...	...	1	...	1	...	1	...	2	...	1	...	...	...	...	6 ,,

case of wilt resistance in cotton, inheritance is complex as in cabbage. Under field conditions, the resistance varies from grades 0 to immunity, being governed by modifying factors. Absence of naturally existing immune types is taken as an evidence for the complexity of inheritance of disease resistance in this case. In the case of rice, resistance to *Piricularia* was found to be complex in inheritance.

Inheritance of reaction to *Fusarium* wilt was studied in bengal gram. A resistant strain 468 was crossed to susceptible strain 19 and the frequency distribution of reactions in the parents and progenies is presented in Table 96.

The distribution indicates simple inheritance. The proportion between the number of readings above and below 20% limit where the two parents merge shows that dominance is incomplete.

8. Breeding for disease resistance.—In cases where disease resistance or immunity is governed by a single pair of genetic factors, it is easy to get homozygous types in F_2 of crosses between resistant and susceptible types. In complex instances the recovery of resistant types in recombined forms is more difficult.

Disease resistant types may be evolved either by straight selection in natural populations or by hybridisation and selection in hybrid progenies. *One important point in any programme for breeding disease resistance types of crops is to select the really immune or resistant type. The selected type must not be an escape.* Selection must be carried out under optimum conditions of infection. In the field the reactions of host plants may be graded as (i) free, (ii) surviving, (iii) killed. Under field conditions, the environment is not controlled and as such the reaction may be varying to some extent and this should not be misjudged as heterozygosity without confirmatory tests under controlled conditions. Every condition that will induce the disease must be provided for, so that there may be no escapes. For this purpose, susceptible types may be inter-planted with the selections under test or in the case of fungoid diseases, spore suspensions may be sprayed at the proper stage of the host plant. In the case of cotton stem weevil, cotton stumps with weevils in different stages of development are interplanted when the seedlings of the selected strains are about one month old. Weevils emerge from old stumps and lay eggs on the new seedlings of the season.

In the case of redgram, selected wilt resistant types are planted year after year in plots where the soil is heavily infected with the fungus. This may be done in all cases where the disease is soilborne. For making selections in rice for types resistant to *Piricularia* the selections may be sown in plots or regions where disease appears year after year and also the susceptible types may be interplanted to induce the disease. Varietal difference in resistance to disease is noticed in this crop. *Korangu samba* and Adt. 10 are susceptible to the disease while Co. 4 and G.E.B. 24 are resistant types. At the Coimbatore Paddy Breeding Station Adt. 10 is interplanted for inducing the disease in field conditions.

The breeder must be sure that the selected types are homozygous for disease resistance and therefore it is essential to test the material under controlled conditions before the type is pronounced as disease resistance. Testing of the selection in green houses is resorted to for the purpose. It must be noted however, that the behaviour of the strain in green house is different from that noted under field conditions. In the case of black stem rust in wheat it was found that varieties which develop types of infection 0, 1, 2 in green house are resistant while those which develop 3, 4 are susceptible. True protoplasmic resistance is more reliable than the resistance based on morphological characters only. *In selecting for disease resistance, the breeder should not loose sight of the primary characters for which the plant is valued by the cultivator.* For example, in selecting wilt resistant types in cotton, yield and quality of the resistant type should not be lost. *Therefore the breeder may carry out selections in the field and these must be further subjected to tests by the pathologist who should grow the selection under heavily infected conditions.* If the material proves heterozygous, further selection is made necessary. If selection proves homozygous and shows 95% resistance it may be released as strain but if it does not prove to be resistant, further selection in that lot is not necessary as this is to be carried out in heterozygous types only. In this connection the decision of the First Conference of Cotton Research Workers in India (1937) may be given here :

"The Conference agrees that the breeding of strains immune to wilt under optimum conditions is the ideal to aim at. For Agricultural distribution resistance of the order of 95% under heavily infected field conditions is satisfactory, provided that the strain has been tested and shown to be practically homozygous for that degree of resistance to wilt.

The Conference recommends that (i) Test for homozygosity should be applied before a resistant strain is released for distribution, (ii) the pathologist should also conduct tests for homozygosity and need only select in material shown to be heterozygous, and (iii) the conditions under which field tests are being carried out should be described and studied as far as is practicable."

Complete homozygosity is difficult to attain and the response to further selection depends upon the degree of selection previously carried out. It has been pointed out that the field technique of Hutchinson and Panse (1936) is the most efficient. The plant breeder must satisfy himself that his selection is homozygous for resistance even under controlled conditions as otherwise it will soon break down.

When the types are not available in the local bulks, hybridisation is resorted to. As in other cases, the yield and other economic characters of the local type are sought to be recombined with the disease resistance found in the wild or introduced type, which latter may not possess other economic characters. The hybridisation and selection in the case of blast resistant strain in rice (Fig. 144), carried out at Coimbatore is detailed here.

In the cross G.E.B. 24 × Korangu samba, selections from F_3 onwards were made based on resistance and homozygosity for other economic characters such as yield. The schedule of selection is presented on the next page :

1929-30 ...	F_3	1,200 families were studied and 450 were selected.
1930-31 ...	F_4	Most of 450 selections did not show disease but were heterozygous for other characters : 40 homozygous types were selected.
1931-32 ...	F_5	Disease absent in all 40 selections. 12 were selected on rough judging for yield.
1932-33 ...	F_6	All 12 were free from disease. One was eliminated because of its heterozygosity in flowering duration.
1933-34 ...	F_7	Regular yield trials with korangu samba as control were conducted. Diseased straw was trampled in the plot and spore suspension was sprayed at heading time to induce the disease. All the eleven selections were free but the control was heavily infested.
1934-35 ...	F_8	Yield trials were conducted at Coimbatore and Aduturai.

It will be of interest to note the nature of inheritance of this disease. The susceptible type Korangu samba was crossed to two of resistant types, *viz.*, G.E.B. 24 and *Co*4. The F_2 ratios are presented in Table 97.

TABLE 97.

	F_2 Ratios.		F_1.
	Diseased.	Free.	
G.E.B. 24 × *K. samba*	248	63	Intermediate.
Co. 4 × *K. samba*	161	311	Resistant.

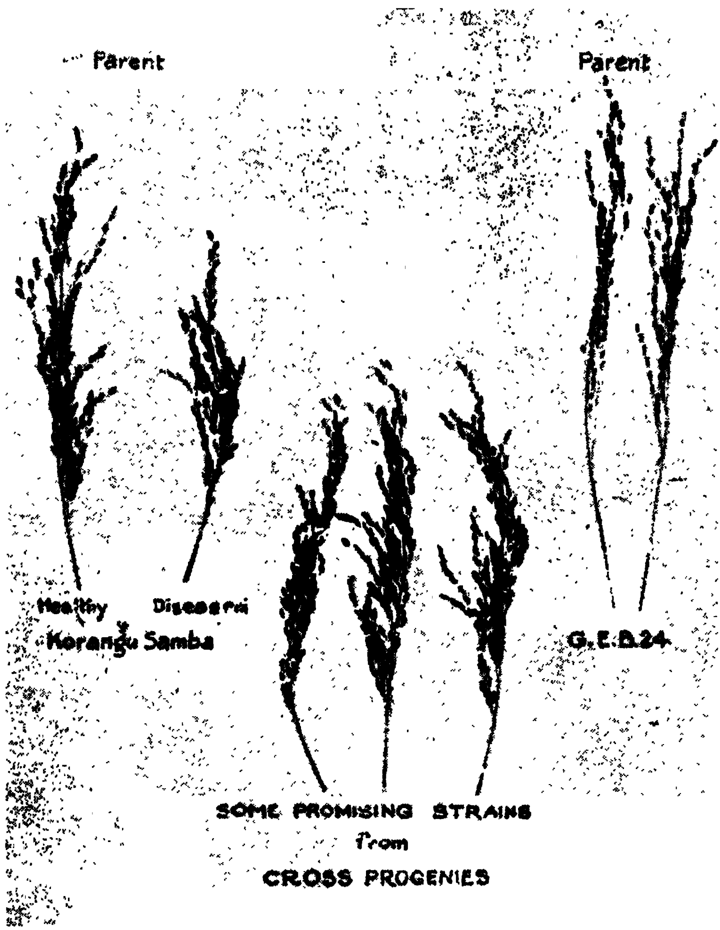
The first cross indicates that resistance is simple recessive to susceptibility while in the second cross the inheritance is more complicated.

In the case of resistance in cotton to *Pempherulus affinis* is by profuse gumming at the wound. Moco which showed high degree of resistance was crossed with *Co*2 which showed susceptibility and selections were made in the hybrid progeny. The quality of *Co*2 and resistance of moco were re-combined in some selections.

In the case of rust resistance in wheat, crosses between *Emmer* ($2n=28$) and *vulgare* ($2n=42$) groups have been widely attempted. In these crosses there is a rapid return to the parental chromosome numbers in the succeeding generations. Sax reported close correlation between 14 chromosome group and resistance and 21 chromosome group and susceptibility. In the progenies all grades of resistance and susceptibility were found and homozygous types for resistance and susceptibility were selected. From the Emmer group, resistance to rust, drought and lodging were transferred to the vulgare group.

By crossing Marquis and Yaroslav, the variety ' Hope ' and *H*44 ($2n$—42) were evolved. They are fertile and externally resemble vulgare type with the desirable qualities of *Emmer* group and these were further used in breeding work. ' Hope ' was further crossed with other cultivated types and its immunity was dominant over susceptibility. The cross with Marquis was governed by two factors while that with ' Ceres ' showed single factor difference. In the case of crosses with other susceptible types, inheritance was complex.

Complex hybridisation was adopted in America for evolving rust resistant varieties of wheat. The variety Thatcher, which was distributed in 1934 is a



(*Photo from Paddy Specialist*).

Fig. 144. GEB 24, Korangu samba and some promising strains from cross-progenies.

selection from a double cross (*Marquis* × *Ilumillo*) × (*Kanred* × *Marquis*). It is widely adapted and superior in quality.

Durum wheats were resistant to stem rust and bunt but since 1925, these diseases are destructive probably due to new forms of *Tilletia tritici*. Similarly new forms of *T. levis* that attack Marquis appeared.

The survey of plant resources of the world carried out by Russian botanist, revealed the existence of valuable plant forms in regard to resistance to pests, diseases, drought and frost. These forms are used as parents in hybridisation programmes. In the case of barley, the chief characteristics of forms in different geographical areas have been mentioned in chapter XII. Hardiness and resistance are usually present in wild forms. Crosses of cultivated types with the wild forms have been largely attempted in evolving resistant types.

In Java, sereh disease was serious and in 1890 Kobus came to India in search of resistant types. He carried 'Chunee' (*Saccharum barberi*) canes which proved resistant to the disease and also yielded resistant P.O.J. progenies on hybridisation with Black cheribon. The mosaic disease was first noted in 1892 in Java. The commercial canes evolved at Coimbatore contain one or two of the following species in their ancestry.

(1) *S. officinarum*—susceptible.
(2) *S. sinense*—some varieties immune and some tolerant.
(3) *S. barberi*—Susceptible but little damaged.
(4) *S. spontaneum*—several forms completely immune.
(5) *S. robustum*—one form which was examined was readily infected.

Among the Java canes, P.O.J. 2725 is fairly resistant. P.O.J. 2727 takes disease rarely and P.O.J. 2878 is highly resistant. Brandes (1925) showed that the immunity is proportional to the amount of *S. spontaneum* blood contained in the commercial type.

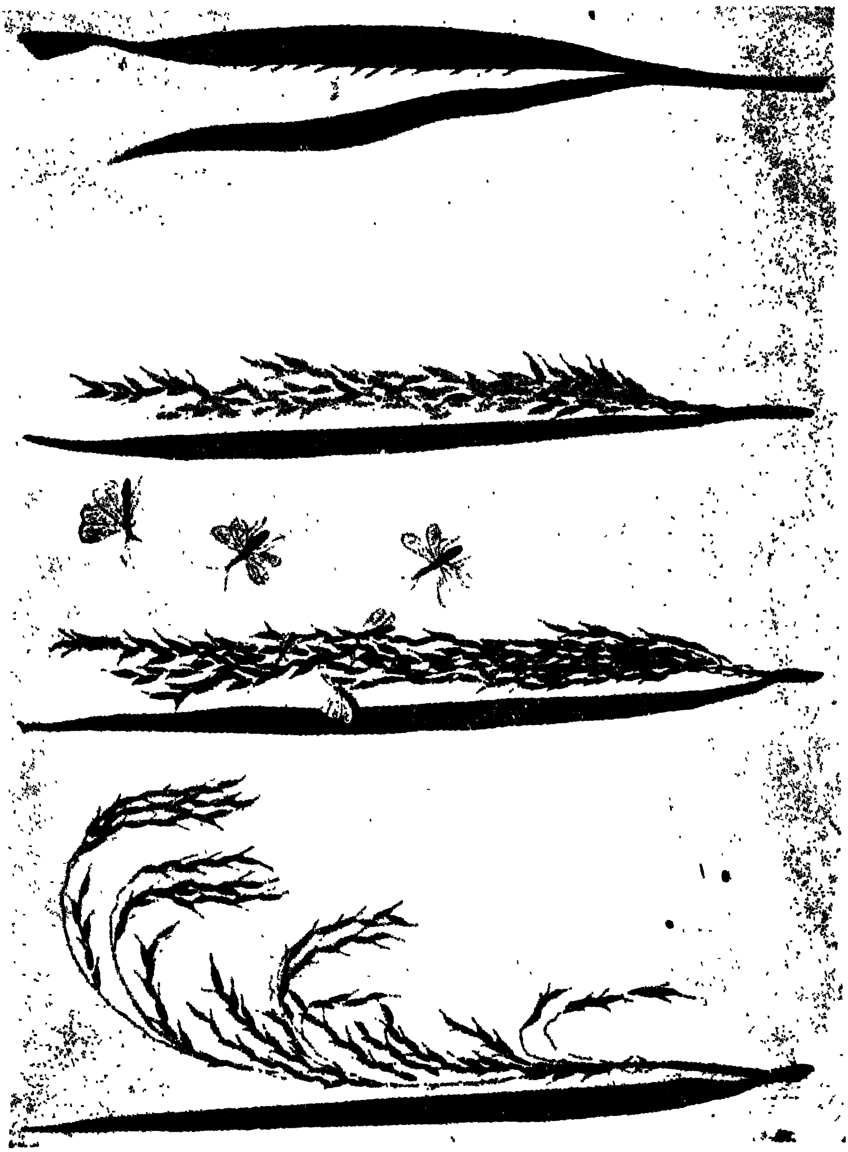
Fig. 145. A. S. 29 Susceptible to *Striga* and (right) *Bonganhilo*, resistant to *Striga*.

There is a great deal of geographical variation in sugarcanes in their resistance to mosaic. Co. 290 is resistant to mosaic in N. India and certain other countries while at Coimbatore it shows 70% infection. Co. 244 is resistant at Coimbatore but it is susceptible in N. India.

In rice, drought resistant type has been selected from the interspecific cross *O. sativa* × *O. longistaminata*. In the case of New World cotton, by Harland's technique of back crossing, resistance to black arm was transferred to *G. barbadense* from *G. hirsutum*.

Another instance where genetical knowledge of the crop is useful in evolving economic type is shown by Sathi (1937). The problem of rice fly infestation is serious in United Provinces and the damage is poor in the type (Sathi) with ears enclosed in leaf sheath. This is a coarse and poor yielding type.

This was crossed with another type and by carrying out selections upto F_8 or F_9, resistant types with yield approaching the normal one were evolved (Fig. 146).



(*With the kind permission of India Government from I. J. A. S.*).

Fig. 146. Selections from hybrid progenies resistant to rice-fly. The parents with the selected types to the centre are shown in the figure.

Striga is sometimes a serious parasite on cholam. At Coimbatore, attempts are made to evolve a resistant type of cholam. The widely cultivated local type A. S. 29, is very susceptible to the parasite. The imported S. African

type, (*Bonganhilo*) is resistant (Fig. 145). A. S. 29 was crossed with *Bonganhilo* and the F_1 was resistant. Some resistant strains have been selected from the hybrid progenies.

In breeding for disease resistance, it is essential that a general survey of local types and wild plants must be carried out and these may be used as parents in hybridisation. Great advances were made in Russia by such a step and the rough classification of selections in respect of disease resistance and other qualities in the case of potato is indicated below :—

FROST RESISTANCE.
S. acaule.
S. anjanhuiri.
S. andigenum.
S. bukasovil.
S. commersonni.
S. curtilobum.
S. demissum.
S. edinense.
S. juzepczukii.
S. millanii.
S. semidemissum.

DROUGHT RESISTANCE.
S. medians.
S. vavilovii.

LATE BLIGHT RESISTANCE.
S. ajuscœnse.
S. antipoviczii.
S. bu bocastanum.
S. demissum.
S. henryi.
S. millanii.
S. polyadenium.
S. vallis-mexici.
S. borrucosum.

VIRUS RESISTANCE.
S. rybinii.

EARLY MATURITY.
S. phureja.
S. rybinii.

SHORT DAY ADAPTATION
S. acaule.
S. antilobum.
S. antipoviczii.
S. bulbocastanum.
S. demissum.
S. goniocalyx.
S. juzpezukii.
S. semidemissum.
S. squamulosum.
S. vallis mexici.
S. verrucosum.

SHORT REST PERIOD.
S. boyacense.
S. Kesselbrenneri.
S. phureja.
S. rybinii.

Disease resistance may be genetically associated with other characters of the plant. Wilt resistance and root characters are associated in cotton. In *Sorghum*, sugary and white grained varieties are more susceptible to stem borers. Plants with juicy stalk and dull mid-rib are having greater tendency for smut than pithy ones.

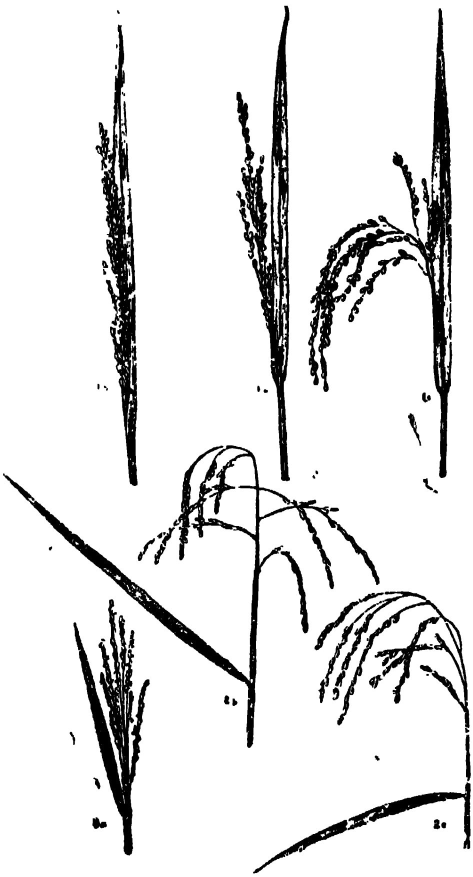
Certain morphological characters may be associated with the incidence of the disease. Identification of these may be helpful in recognising the resistant or susceptible type in the field. In the case of *Piricularia* disease of rice, the following morphological characters have been studied:

(*a*) *Size and inclination of shot blade.*—An infected flag is a menace to the ear by nursing the fungus, sending down its spores and easily infecting the ear. In general, the susceptible types show erect and broad blades.

(*b*) *Emergence of the ear.*—Short emergence facilitates easy infection of the ear. Therefore, lengthy emergence is associated with resistance.

(*c*) *Spread of panicle.*—Well spread out panicles show less tendency for spore infection and are therefore associated with resistance. Closely packed ear-head shows greater tendency for infection. Table 98 shows the relationship between morphological characters and disease resistance.

It is to be noted that those varieties with reclining shot blade, long emergence, and spreading panicle are the most resistant (Fig. 147).



(*With the kind permission of M. A. J.*).

Fig. 147. Varieties of rice susceptible to *Piricularia*. These varieties possess broad and erect flags. Resistant types with reclining flag, emergence and spreading panicle are shown in the bottom row.

From the analysis of the problems relating to breeding for disease or insect resistance in plants, the position appears to be rather intriguing. The plants show varying amount of resistance which is gene controlled ; similarly, the pathogen—the insect or the fungus—shows varying amount of power to attack the host plant and this capacity of the pathogen is also gene controlled. Thus, the breeder deals with two biological variables. Hitherto, the breeders were evolving pure strains valued for their yield or quality of the produce. This

TABLE 98.

No.	Variety.	Incidence of disease—%	Area of flag.		Area of penultimate leaf.		Inclination of the flag in degrees.		Emergence of the ear.		Nature of Panicle.
			Length—cm.	Breadth—cm.	Length—cm.	Breadth—cm.	Flower stage.	Ripe stage.	Flower stage.	Ripe stage.	
1	G. E. B. 24	0·1	29·3	1·07	39·0	0·83	17 1	94·5	7·0	7·1	Spreading.
2	*Co.* 1	0·5	33·8	1·01	41·4	0·80	6·5	78·0	6·0	6·6	Do.
3	E. B. 301	2·9	32·3	1·82	48·3	1·68	73·0	93·5	2·1	4·3	Medium.
4	*Co.* 2	23·1	41·7	1·54	60·6	1·05	8·0	37·0	0·7	2·0	Do.
5	*Co.* 3	24·1	37·0	1·39	57·5	1·05	4·5	30·5	1·3	8·2	Do.
6	*Sadai samba*	24·2	34·9	1·19	46·5	1·00	15·5	52.0	3·5	7·1	Do.
7	Adt. 2	78·2	35·5	1·17	50·7	0·97	11·5	15·0	—0·4	5·5	Do.
8	Adt. 1	73·1	34·5	1·31	45·1	1·05	9·5	19·0	—0·6	6·3	Do.
9	*Korangu samba*	73·5	33·4	1·36	50·8	1·06	5·5	3·0	—2·75	4·0	Close.
10	*Nellore samba*	13·0	34·4	1·39	49·2	1·24	6·0	12·5	—1·2	1·0	Medium.

naturally results in narrowing down the variability of the new strain. The naturally existing pathogen remains widely variable and hence is always in an advantageous position to attack the pure strain. In Nature, there is a sort of balance between the host and the pathogen : *When all the susceptible types of a mixed population are destroyed, the resistant types multiply* ; *naturally the pathogen is placed in a disadvantageous position* ; *but this change on the part of the host acts as a selection on the pathogen and a new genetic type which can attack the resistant type is selected.* This balancing goes on alternately. Selection of improved types by the plant breeder, as already pointed out, leads to narrowing down the genetic variability of the plant and widens the scope for destruction by the variable pathogen. Analysis of the genetics of both the host and the pathogen seems to be the only solution for the problem.

So long as the pathogen remains genetically variable in Nature, the breeder is forced to accept the need for variability in the selected strain also. A perfectly homozygous type in respect of all characters seems to stand the risk of quick elimination.

This need for variability in the selected strains is now being recognised by the plant breeders, who were once keen in attaining high degree of homozygosity by selfing the selected strains over a number of generations. Reference may be made to the work of Harland in Peru. He started with a large number of plants, tested individually for a small number of commercially valuable characters and selected for these only, leaving all other characters as variable as possible. He avoided selfing which resulted in homozygosity for all characters.

9. **Achievements.**—Plant breeders in India have evolved resistant types to the various important diseases of crops in this country. The following are a few diseases for which breeding is carried on.

TABLE 99.

Wheat ...	Stem rust ...	*Puccinia graminis* Pers.
	Yellow rust ...	*P. glumarum Schm.*
	Brown smut ...	*Urocystis triticina* Erikes.
	Flag smut ...	*U. tritici Koern.*
	Loose smut ...	*Ustilago tritici* (pers).
Barley ...	Smut	*Ustilago Hordei* (Pers) Ingerheim.
Oats ...	Smut	*Ustilago Kolleri.* Wille.
Rice ...	Leaf spot	*Piricularia oryzeae*, Cavara.
Cotton ...	Wilt	*Fusarium vasinfectum* Atk.
	Root rot ...	*Macrophomina phaseoli* (Maub) Ashby.
Pigeon peas ...	Wilt	*Fusarium udum.* Butler.
Sunnhemp ...	,, ...	*F. udum.* Butler, var. *Crotalarieae* (Kulkarni) Padwick.
Gram ...	,, ...	*F. orthoceras*, Appel Woll. *Var. Ciceri* Padwick.
	Foot rot ...	*Operculella Padwickii*, Kheswalla.
	Blight	*Mycosphaerella rabieii*, Kovachevsky.
Potatoes ...	Late blight ...	*Phytophthora infestans*, de Bary.
	Early blight ...	*Alternaria solani* (Elb et. Mart. Jones et Gr.).
Sugarcane ...	Red rot	*Collectotrichum falcatum* Went.
	Smut	*Ustilago scitamineae*, Sydow.
	Wilt	*Cephalosporium Sacchari*, Butler.

A list of resistant strains, evolved at various centres in India is herein furnished. (Table 100).

TABLE 100.

LIST OF DISEASE—RESISTANT VARIETIES.

—(*From Proc. Ind. Acad. Sc.*)

Variety.	Nature of Resistance.	Name of Disease.	Tract in which it is disease resistant.	Remarks.
WHEAT.				
Pusa 114	Highly resistant ...	Rust disease due to *Puccinia graminis*, *P. triticina* and *P. glumarum* and loose smut due to *Ustilago tritici*.	Sind (not tried elsewhere).	
Do. 80-5	Do. ...	Rust disease due to *Puccinia graminis*, *P. triticina* and *P. glumarum*.	General	
Do. 120	Do. ...	Do. ...	Do.	
Do. 165	Do. ...	Do. ...	Do.	
Do. 4	Resistant ...	Do. ...	Do.	
Do. 12	Do. ...	Do. ...	Do.	
Do. 52	Do. ...	Do. ...	Do.	
Do. 101	Do. ...	Do. ...	Do.	
Do. 111	Do. ..	Do. ...	Do.	
C. 121	Complete immunity ...	Yellow rust *P. glumarum*....	Lyallpur.	
C. 591	Low susceptibility ...	Yellow and black rust (*P. glumarum* and *P. graminis*).	Do.	Hybrid line.

9D	Almost complete immunity.	Loose smut (*Ustilago tritici*)	Lyallpur	Improved wheat for *barani* conditions.
8B	Low susceptibility	Yellow rust (*P. glumarum*).	Do.	
T11	Do.	Black rust (*P. graminis*)	Do.	
8A	Do.	Bunt (*Tilletia indica*)	N.W.F. Province	The varieties are given in descending order of susceptibility.
Pusa 4	Do.	Do.	Do.	Do.
C. 518	Do.	Do.	Do.	Do.
Pusa 52	Do.	Rust diseases	North Bihar.	
Pusa 114	Do.	Do.	Sind.	
C. Ph. 47	Do.	Do.	North and middle Sind.	
Sind A. T. 38	Do.	Do.	Northern Sind.	
Sind HSW III	Do.	Do.	Eastern Sind.	
PADDY.				
Pusa *T18*	Resistant	Piricularia (*P. oryzeoe*)	Not tried on large scale.	Early variety.
Sathi	Completely immune	*Leptocoriza varicornis*	United Provinces	Immunity due to the sheath cover protecting the ear.
GEB 24	Highly resistant	Paddy blast (*P. oryzeae*)	Coimbatore, Aduturai and many other places where it has spread.	Susceptibility reported from Coorg. Large supply of *N.* reduces resistance.
Do.	Completely immune	Foot rot (*Fusarium moniliforme*).	Coimbatore, Maruteru, etc.	
Do.	Low susceptibility	Stemborer (*Schoenobius incertellus*).	Maruteru	Late sowing reduces resistance.

TABLE 100—(*Contd.*)

Variety.	Nature of Resistance.	Name of Disease.	Tract in which it is disease resistant.	Remarks.
Co. 1	Highly resistant ...	Paddy blast (*P. oryzae*) ...	Coimbatore, Aduturai ...	Not so widely spread as GEB-24 outside Coimbatore.
Do.	Do. ...	Foot rot (*F. moniliforme*)...	Coimbatore, Maruteru.	
Co. 4	Completely immune ...	Paddy blast (*P. oryzae*) ...	Coimbatore and Áduturai.	
Krishnakatukulu ...	Low susceptibility ...	Foot rot (*F. moniliforme*).	Maruteru and Coimbatore.	Godavari delta variety.
Akkullu	Do. ..	Do. ...	Do. ...	Do.
Nullarlu	Do. ...	Do. ...	Do. ...	Do.
Atragada	Do. ...	Do. ...	Do. ...	Do.
Vankisannam	Do. ...	Do. ...	Do. ...	Do.
Wateribune	Do. ...	Do. ...	Do. ...	An American variety.
Aryan	Highly resistant ...	Do. ...	Do. ...	Malabar variety.
JOWAR.				
J. 301 and J. 8 ...	Low susceptibility ...	Red leaf	Punjab	In very humid years the resistance is lowered.
J. S. 21	Do. ...	Red leaf spot and smut ...	South-Eastern Punjab.	Do.
Imphie and J. S. 20 ...	Very low susceptibility...	Do. ...	Do.	
Sind allakh and Sind Allakh × Torh hybrid No. 4, 54, 339, 109.	Do. ...	Stem-borer	Sind.	
Bonganhilo and Bilichigan.	Resistant	*Striga Sp.*	Coimbatore.	

BARLEY.				
Pusa, T. 21	Resistant	Stripe disease (*Helminthosporeum Sativum*).	North Bihar. Not tried elsewhere.	
Plumage Archer ...	Complete immunity ...	Black and Yellow rust ...	North-West Frontier Province.	
OATS.				
B. S. 1	Resistant	Covered Smut (*Ustilago Kolleri*).	North Bihar (Not tried elsewhere).	
LINSEED.				
Pusa T. 12	Low susceptibility ...	Rust (*Melamsora lini*) ...	North Bihar.	
Do. T. 121	Do. ...	Do. ...	Do.	
Pusa T. 124	Do. ...	Rust (Melamsora lini). ...	North Bihar ...	Mutant from T. 12.
S. 6	Complete immunity ...	Do. ...	South-eastern Bihar.	
P 12	Do. ..	Do. ..	Do.	
Hybrids 1150, 1193, 1206 and 1196.	Do. ..	Do. ...	United Provinces ...	With high seed and oil yield.
GROUND-NUT.				
K. 17	Low susceptibility ...	Tikka leaf spot—(*Cercospora sp.*)	Bihar and Orissa.	
COCONUT.				
Philippine variety ...	Low susceptibility ...	Shoot-rot (*Glœsporium sp*).	West-coast Madras.	
SOYABEANS.				
Pusa Yellow	Low susceptibility ...	Root-rot in early stages and white ant in later stages.	Sind.	

TABLE 100—(*Contd.*)

Variety.	Nature of Resistance.	Name of Disease.	Tract in which it is disease resistant.	Remarks.
SAFFLOWER.				
Pusa types, 9, 17, 18 & 19.	Complete immunity ...	Frost	Sakrand.	
Mixed Pusa—H. 68 & H. 12	Do. ...	Do.	Do.	
Dhollra 1—Raichur ...	Low susceptibility ...	Do.	Do.	
RED GRAM.				
Pusa types, 16, 41, 50, 51, 80 & 82.	Highly resistant ...	Wilt due to *F. vasinfectum*.	North Bihar. Not tried elsewhere.	
Comilla, white, black, brown and crimson.	Low susceptibility ...	Wilt due to *F. udum* ...	Bengal.	
S2 & S7	Do. ...	Wilt	North Bihar.	
BENGAL GRAM.				
Karachi	Complete immunity ...	Wilt—*Fusarum sp.* ...	Mouywa, Kyankse, Yamethu districts in Burma.	
Do.	Low susceptibility ...	Do. ...	Central Provinces.	
W. R. 18	98% resistant	Do. ...	Dharwar.	
Coimbatore types, 416, 468 & 482.	Low susceptibility ...	Do. ...	Coimbatore (Madras).	

SUNN-HEMP.				
D—IX	Complete immunity ...	Wilt–*Fusarium vasinfectum*.	Bombay	Homozygous resistant under all conditions.
JUTE.				
D. 154	Complete immunity ...	Chlorosis	Bengal.	
COTTON.				
G. peruvianum varieties from S. America, Verdan, Quebra—Dinho and Moco.	Very low susceptibility ...	Stem Weevil (*Pempheres affinis*.)	Coimbatore, Madras. ...	These are late varieties with bad opening and susceptible to jassids.
G. hirsutum Cambodia *Co*. 2.	Practically immune ...	Jassids	South and Central India and S. Africa.	
Bengal, Cawnpore, Banila, Bengali, 85—10 (13), 58·16 (3), Garohil, Dacca muslin.	Low susceptibility ...	Wilt–*Fusarium vasinfectum*.	Bengal.	
America, Cambodia, KA1, 73·40 *c*, 7 (10), 41·30·9 (19) Akola Buri, Extra early Buri and 289 F.	Do. ...	Do. ...	Do.	
G. herbaceum Jayawant ...	92% resistant	Do. ...	Bombay, Karnatak ...	Soil temperature of 22—27·C lowers resistance.
B. D.—8	Highly resistant only shows root discolouration in 1—8% of plants.	Do. ...	Broach District, Bombay.	Do.

TABLE 100—(*Contd.*)

Variety.	Nature of Resistance.	Name of Disease.	Tract in which it is disease resistant.	Remarks.
G. hursutum Gadag 1 ...	60% resistant	Red leaf blight ...	Dharwar.	
Buri	Complete immunity ...	Wilt *Fusarium vasinfectum*.	Nagpur.	
Verūm 262, 436 and late verum.	Low susceptibility ...	Do. ...	C. P. and Berar.	
Roseum and Bani ...	Do.	Anthracnose	Do.	
SUGARCANE.				
Co. 205	Highly resistant ...	Mosaic	Coimbatore	Reported to be susceptible at Pusa and other places.
Co. Nos. 214, 244, 314, 315, 316, 318, 335, 351, 355, 356, POJ 2878.	Immune	Do.	Do.	Not reported to be susceptible elsewhere.
Co. 214	Do.	Do.	Bihar and Orissa.	
Co. 205, 210, 213, 281, 285.	Highly tolerant ...	Do.	Do.	
H.M. Nos. 320, 487, 544, 607—609.	Do.	Do.	Do.	
D.S. 1, 8, 19, 23—25 & 27—35.	Low susceptibility ...	Do.	Bengal.	
Thin varieties are more susceptible than thick canes.	Do. ...	Smut (*Ustilago sacchari*) ...	Coimbatore (Madras)	
Co. 205, 210 & 214 ...	Do. ...	Do.	Bihar and Orissa and U.P.	

Co. 285	Low susceptibility ...	Smut (*Ustilago sacchari*) ...	N.W.F. Province and United Province.	
Co. 290	Complete immunity ...	Do. ...	Do.	
Co. 290	Do. ...	Red-rot *Colletotrichum falcatum.*	N.W.F .Province and United Province.	
Co. 285	Low susceptibility ...	Do. ...	Do.	
Co. 205, 214, 285 & 299 ...	Do. ...	Do. ...	Bihar and Orissa.	
Co. 205, 213, 214, 281, 285 and 326.	Do. ...	Top-rot *Melanconium sacchari.*	Do.	
Co. 214	Resistant	Insect attack (Pyrilla) ...	Do.	
Co. 285	Low susceptibility ...	Stem borer	Do.	
TOBACCO.				
Adcock, cash, shade Pusa type.	Resistant	Wilt (*Phytophthora parasitica*).	Coimbatore ...	Have shown resistance under laboratory conditions.

Chapter 21

PHASIC DEVELOPMENT IN PLANTS

INTRODUCTION—LYSENKO'S THEORY—FIRST PHASE—SECOND PHASE—THIRD PHASE—PHYSIOLOGY OF VERNALISATION—THE TECHNIQUE—VERNALISATION OF SOME CROPS—GENETIC CONCEPTIONS.

1. Introduction.—The plant breeder aims at selecting new types of plants that are best fitted to the tract. He may be required to select for high yield of grain or vegetative part, earliness, drought resistance or for extending cultivation to new regions. The exploration of the plant world in different economic aspects has been in progress since many years but with the development of genetics and cytology the art of selection came to be based on certain fundamental conceptions. On account of this, selection of new types was rationalised with the dawn of twentieth century. The various concepts centred round the physical bases of heredity and most of the breeders were concerned with the change of nuclear contents, *viz.*, the genotype. The growth and development of the plant, especially the manifestation of the morphological features, were considered to be governed by genotype and the environment had to play a minor role within limits. All characters of the plant, including vegetative growth, reproduction, earliness or lateness of flowering, etc., were taken to be governed by mendelian factors.

It was realised since 1913 (Klebs) that growth and development constitute two major aspects of plant life and that one is to be distinguished from the other. The inter-relationship between growth and development was variously interpreted and it was even thought that one is antagonistic to the other. Klebs was the first to realise the fact that the flowering duration of a plant is not an inherent character but that it could be altered by environmental factors like light, etc., Garner and Allard (1920) studied the relation between the duration of light and darkness and its influence on the plant. This is termed photoperiodism. They divided plants into the following classes (1) *Long-day plants which progress to maturity quickly under long-day conditions.* (2) *Short-day plants which do so under short-day conditions.* (3) *Plants which are indifferent to the changes in the light period.* According to this, there is a critical duration of light above which long-day plants come to flowering and below which short-day plants come to flowering. Different species or even varieties and strains within a species show different photoperiodic responses and Eghis (1928) found that if Soya bean plants were first exposed to conditions of short-day for several days they come to flower earlier than control even if they were grown later under long-day conditions. This is known as *photoperiodic induction* or *photoperiodic after effect.* It will thus be seen that the onset of flowering in plants is governed by certain environmental conditions. A knowledge of this aspect is essential to a plant breeder for the reason that grain yields depend on flowering and fertility. Further, the fact that the relative length of day and night, *i.e.*, light and darkness—has pronounced influence on the onset of flowering, implies geographical limitation to the

spread of a crop. In regions of short day and long nights, the long day plants fail to flower. Even seasonal changes in the same region may affect flowering. Thus, winter wheat sown in spring does not ear in the same season. This is a serious problem in the extreme climates of Europe and Asiatic plains of U.S.S.R. The physiology of the failure of flowering was studied by Lysenko and he developed new conceptions regarding growth and development. He also advocated certain pre-treatment to seeds before sowing, termed *vernalisation* which altered the relationship between the plant and its environment. By such pre-treatments many advantages such as increased yield, extension of cultivation to new regions, etc., have been achieved in Russia in respect of different crops as wheat and cotton. Lysenko's theory of phasic development is not only important in its practical application but also bears new conceptions in the field of plant physiology and genetics and these will be dealt with in the following pages.

2. **Lysenko's theory.**—Development of a plant and its growth are independent of each other and have different environmental factors. *Factors determining development are different from those determining growth but they are not antagonistic to each other. Development need not be concurrent or subsequent to growth.* The length of vegetative period is not fixed for a plant. Growth indicates increase in weight and size of a plant and the external morphological features are no indications of internal development. *The nature and magnitude of factors governing development are different in different plants and according to Lysenko, these factors may be allowed to act on the germinating seed or growing plants. The duration of treatment varies with different plants. Therefore the process of sexual development is determined even in the germinating seed and is separated in time from growth.*

It has been pointed out that photoperiodism has a pronounced effect on the onset of flowering. There are two other theories regarding the onset of flowering. (1) hormone theory, (2) C/N ratio theory. Rasumov and Maximov put forward a theory that there is antagonism between reproductive development and vegetative growth of a plant. Ljubimenko (1933, 1934) experimented with pea embryo without cotyledons and with lupin defoliated in various ways showed that growth has no effect on development. When the seed is soaked and germination starts, the plant is purely in a vegetative phase but very soon growth and development proceed concurrently. Long before visible changes take place in size and form due to growth, internal re-adjustments occur in the seed. While many of the physiologists experimented with grown-up plants where curtailment of a factor such as light visibly affected photosynthesis and consequently increase in size, Lysenko experimented with germinating seed in which light could be cut off without detrimental effect to subsequent growth. Lysenko brought out the distinctness of growth and development. Lysenko further postulated that the development of a plant has five phases. *These developmental phases occur in strict sequence and each phase has its own optimal environmental factors.* When conditions for completion of a developmental phase are not fulfilled, the plant progresses up to that phase only and no further. *The plant proceeds from one phase to another in strict sequence only.* Of the five stages of develop-

ment only three stages are known (1) *vernalisation* or *thermophase* or *first phase*, (2) *photo-phase* or *second phase*, (3) *the third phase* is connected with gameto-genesis. The factors affecting the third phase are not known.

3. **First phase.**—The term vernalisation, the original Russian equivalent of which is jarovizatie, signifies (1) the first stage of development and (2) the technique of pre-treatment of seed by Lysenko by which the flowering phase of a plant is forced earlier. There are many other synonyms of the term, such as, yarovisation, jarovisation, Iarovatsii, Irovization, springification and springisation.

The first phase or vernalisation phase leaves no morphological traces on the plant, (*i.e.*, the germinating seed) but is connected with a definite decrease in the temperature of the medium. When this temperature limit is exceeded, the plant remains sterile. By chilling the germinating seeds of wheat and barley, Lysenko showed that the length of day during subsequent growth has no effect on the on-set of flowering. There is a minimum period of chilling for each crop ; for wheat 38 days and for barley 28 days, to overcome the retarding effects of temperature during subsequent growth. Similarly in the case of cotton, Lysenko showed that high temperature is not actually required for the formation of flower buds, but seedlings kept at 25°—30°C for 15-20 days flowered when raised at 10°—15°C. The high temperature that is required for completion of developmental phase that leads to flowering, may be satisfied even at the seedling stage or even before sowing, by keeping the germinating seed at high temperature. When so treated, the plants flowered at low temperature while the controls raised at low temperature failed to flower.

Though growth and development are independent, the vernalisation phase can be completed only after the seed is germinated, *i.e.*, a minimum of growth has taken place. Not all factors of environment have equal influence on vernalisation. "*Conditions of the habitat*" have to be distinguished from "*influencing factors*". Some factors may quicken the process of vernalisation and in the absence of such stimulants vernalisation may proceed normally; but there are certain indispensable conditions under which only vernalisation can proceed and any deviation from these inhibits vernalisation irrespective of the presence of stimulating factors. Among the latter are increased pressure of oxygen, 0.1-0·001% ethylene, ethylene bichloride, chloroform, sulphuric ether and other gases. It has been already pointed out that the manifestations of morphological characters or *morphogenesis* are features subsequent to qualitative developmental changes that take place inside a plant. There are as yet no methods by which the developmental phases could be studied morphologically. However, certain bio-chemical tests have been developed by which the completion of first phase could be tested.

The first phase, as well as other subsequent phases is governed by a set of environmental factors such as temperature, moisture and light. They are interrelated by compensating gradations. Certain plants such as millet, soyabean, etc., require high temperatures from 20°—30°C, while others like grasses and other cereals require low temperatures for completing the first

phase. There is no strict demarcation between the two groups of plants. For all plants, two critical limits exist—the upper and the lower limits. When the critical limits are exceeded vernalisation is inhibited. For example, wheat was vernalised by Lysenko (1937) in 40 days at 0—2 °C and in 10—15 days at 15°—20 °C. At higher or lower temperatures, vernalisation was inhibited. There is evidence to show that the temperature treatment of the first phase can be given in instalments, the actual period required for vernalisation remaining constant. However it is suspected that too frequent alternation of temperatures may inhibit vernalisation.

The object of the vernalisation treatment is to complete the first phase and second phase when the embryo is physiologically alive but not dependent on external environment for its nourishment. *Therefore, the moisture content of the seed is kept at such a level that will make the embryo active but not grow rapidly.* Moisture is required both for activating the embryo of the dry seed and also to fulfil the first phase. Below certain minimum level it inhibits vernalisation and above a certain maximum level it leads to active growth in size of embryo and the continued vernalisation treatment becomes difficult and complicated. Various buffer solutions have been proposed to arrest growth during vernalisation but objection to their use have been raised on the score that such retardation of growth may affect the progress of vernalisation. In addition to temperature and moisture, the presence of oxygen is found to be an essential factor for vernalisation. The duration of the first phase is not a fixed quantity for any one variety and it is different for different regions and sowing periods. *It is therefore to be understood that the vernalised plant reacts differently to the environment as compared to unvernalised plants.* The length of first phase should not be judged by its effect on shortening the vegetative period or hastening flowering. This is particularly so, after the discovery of the possibility of vernalisation during seed ripening. Considerable development has of course already occurred in the embryo during fruit formation and the behaviour of the plants after sowing depend on how far this embryonic development had proceeded.

4. **Second phase.**—The second phase is connected with the light requirements of the plant and hence is also termed photophase. The pronounced effect of light on flowering has long been recognised. Garner and Allard (1920) pointed out that the length of day and night has pronounced effect on the onset of flowering. Evidently some internal chemical changes take place which stimulate the development of floral buds in the place of vegetative buds.

The foregoing conceptions of photoperiodic effect have been revised by Lysenko's experiments on vernalisation. Long-day plants require continuous period of light and short-day plants require continuous period of darkness to complete the second phase. When these periods of light and darkness are applied to vernalised seeds, the plants flower irrespective of day lengths during further growth of vernalised seeds. It has been shown that there is no antagonistic after-effect of long-day or short-day plants and *vice versa*. Razumov (1933) showed that the long wave region of the solar spectrum, especially the

red rays, fulfilled the light requirements while short wave light such as green, blue and violet were equivalent to darkness.

Regarding the other environmental factors that have pronounced effect on the completion of second phase, temperature, moisture and aeration are important. How far these are biologically indispensable for the second phase has not been clearly understood. The duration of second phase depends upon the various combinations of the environmental factors and is also a varietal character. There is at present no definite method by which the beginning or completion of second phase could be tested.

5. **Third phase.**—Though Lysenko indicated the possibility of five developmental phases, he has mentioned the first two only. After completing the first phase, the plant enters the subsequent phases each of which has definite environmental conditions.

Kiricenko (1934) indicated the third phase and his experiment is as follows :

Vernalised winter wheat was divided into the following three groups.

A. grown in continuous day for 44 days.
B. grown in 12 hours day for 44 days.
C. grown in 10 hour-day for 44 days.

12 plants from each series were subject to 2 to 12 hours photoperiods in the subsequent 34 days. B & C did not flower. Plants belonging to group A flowered but those subject to 2 to 4 hour photoperiods failed to form normal pollen grains. By further experiments with wheat it was found that a short period of light is required for the formation of normal pollen grains.

6. **Physiology of vernalisation.**—There is no morphological difference between the vernalised and unvernalised plants but they are internally differentiated as shown by their flowering behaviour under long or short day conditions as the case may be. Melijnikov (1936) showed that under the first phase, certain photosynthetic chromidia and plastids are formed which lead to development of chlorophyll under the second phase. Thus, increased chlorophyll content of leaf in vernalised wheat was found. Bassarskaja (1934, 1936) pointed out that in the process of vernalisation the physical and chemical properties of protoplasm change. This is shown by the fact that the promeristem after vernalisation of the first phase plasmolysed at a higher salt concentration, showed difference in staining reaction and increased permeability. By staining reactions of vernalised plants it was found that the second phase does not begin until the first is completed and that the differentiation attained by the tissues is not lost if the onset of second phase is delayed due to environmental conditions, *i.e.*, the process appears irreversible.

Lysenko is opposed to the theory that the effect of vernalisation is due to the production of certain hormones. According to the supporters of hormone theory the flowering of winter wheat is due to the inhibiting effect of some hormone ; and the flowering of the same after vernalisation is attributed to the production of winter hormone. Cholodny (1936) states that the endosperm of soaked seeds produces a hormone termed *blastinin*, which is imbibed

by the embryo. Because the embryo is not actively growing during vernalisation, the hormone accumulates in embryo. The accumulation of the unexpended blastinin hastens development when the embryo begins to grow. Purvis (1944) showed that excised embryos can be vernalised. The seat of production of the hormone may be embryo itself.

The other hormone theory as proposed by Gregory and Purvis (1937) is as follows :—

A is a precursor which is converted into B at low temperature.

B, depending upon day length and temperature is converted into C, a flower initiating substance or into E, a vegetative leaf promoting substance.

The reaction B to C is reversible and as such during the process of devernalisation in drying seed and in subsequent growth, conversion of C into E through the intermediate B stage takes place. The chain of reactions is diagrammatically shown below.

$$\begin{tikzcd} & & E \text{ leaf promoting substance.} & & \\ \text{Precursor} & A \arrow[r] & B \arrow[u, dashed] \arrow[r, shift left, "\text{short-day}"] & C \arrow[l, shift left] \arrow[r, "\text{long-day}"] & D \end{tikzcd}$$

Crushed tissues of vernalised seeds failed to show the presence of such hormones.

Enzyme changes during the process of vernalisation were studied by many investigators. Mainly catalases and peroxidases differed in the vernalised and unvernalised seeds. In rice both diastase and catalase increase during vernalisation. The treatment in light has caused greater increase than that in darkness. In the former treatment catalase decreases slowly until it is equal in both. When the seeds are germinated, the increase in diastase is greater and that in catalase is less than those of untreated germinating seeds. Schander (1934) showed that in cereals, a substance is transferred from aleurone layer to the embryo in the first few hours after soaking. In rice it was found that the translocation of the substance takes place within the first six hours after soaking. By ringing tests it was found that a mere contact of bran is sufficient for this translocation.

The physiological changes during vernalisation can also be judged by the difference in staining reactions and iso-electric point of the pro-meristematic tissues of vernalised and unvernalised seeds. The tests are carried out as follows :—

(i) Sections of embryo cut at thickness of 75μ using freezing microtome.

(ii) Sections mounted using a gelatine fixative.

(iii) Slides treated with 5% ferric chloride for 3 minutes with 5% potassium ferrocyanide.

With the progress of vernalisation, the growing point changes from yellow to green and then dark blue while tissues other than growing point stain blue from the beginning.

Change of iso-electric point is tested as follows :—

(1) Embryos sectioned and mounted as previously outlined.

(2) Slides treated for 15 minutes with McIlvaine's buffer of pH 3·6 to 7·0 with intervals of 0·2.

(3) Sections stained for 5 minutes in an aqueous solution formed by mixing equal volumes of 1 % solution of eosin and 1 % solution of methylene blue at the moment of staining.

(4) After staining, slides rinsed in distilled water and returned to buffer solutions for 6 hours.

(5) At conclusion of 6 hours, the pH of buffers determined using a Coleman glass electrode apparatus.

In the case of Marquis wheat, at pH 5·32, sections from unvernalised seeds stained blue. At 4 days' chilling, it stained at pH 5·13 and when vernalisation was complete it stained blue at pH 4·88 thus indicating that iso-electric point changes from pH 5·32 to pH 4·88 during vernalisation.

Similar tests for the completion of phases 1 and 2 have been mentioned in Imperial Agricultural Bureau Bulletin No. 17, 1935.

7. **The technique.**—When the embryo of a resting seed is activated on soaking in water, the embryonic cells begin to divide and increase in number and size. In addition to this vegetative phase, if environmental conditions are favourable the cells pass through successive developmental phases which ultimately lead to flower and fruit formation at the shortest period from germination. Growth and development may differ in their optimal requirements of environmental factors and therefore under natural conditions they proceed at different rates. Lysenko's technique of vernalisation aims at providing optimal conditions to the germinating seed that will hasten the completion of the first two stages, *viz.*, thermostage and photostage and in the process, growth is checked to the maximum limit. When such treated seeds are sown, growth progresses and because the first two phases of development have already been completed, the plants flower and fruit earlier than untreated seeds.

The optimal conditions that hasten the completion of the first two phases vary with different plants and varieties of the same species. Therefore it is necessary to determine the exact conditions for each crop before the process can be adopted on any large scale. These conditions have been studied in respect of many crops mainly in Russia and to a smaller extent in other places. Thus in respect of wheat, which could be grouped into winter, semi-winter and spring forms, the following ranges of temperature for completion of first phase have been noted.

Winter forms : not lower than 2 °C and not over 10 °C.

Semi-winter forms not lower than 3 °C and not over 15 °C.

Spring forms not lower than 5 °C and not over 20 °C.

Though these three forms of wheat are agriculturally recognised vernalisation tests have not shown them to be distinct groups in respect of their temperature requirements and one group merges into the other.

The vernalisation process mainly consists of the following steps :—

The seeds are soaked in water for a limited period with the object of breaking the dormancy of the embryo of the dry seed. As already pointed out, phasic development can take place only in active pro-meristematic cells. The soaking is limited to such periods that will only activate the embryo of the seed but not allow it to grow rapidly. In respect of each variety the moisture content that will maintain the embryo active but not allow it to grow rapidly may be expressed as percentage. The seed is then subjected to low temperature. There is a definite range of temperature for this chilling with a lower and upper limit. If the temperature is beyond the range then the seed does not successfully complete the first phase and hence the winter form when sown in spring does not ear. The duration of the treatment is also a varietal character. Lysenko indicates the following formula :

$$n = \mathrm{A}/\mathrm{B}-t$$

Where n is the duration of the phase in days, B is the maximum temperature beyond which the phase will not progress and t is average daily temperature and 'A' represents the sum of differences between B and the daily environmental temperature during the duration of the phase. In the case of one Russian variety of wheat, Lysenko reports the following values :

$$A=300 : B=12\,°C.$$

For *Hordeum pallidium* the values are $A=350$; $B=15\,°C$. As the temperature of the medium approaches B, the duration of treatment becomes longer and longer and when the temperature exceeds B, the variety does not ear. There is a minimum period of treatment in respect of each crop which is to be determined by actual experiment. The chilling treatment is followed by photo stage. The seeds are subjected to continuous light in the case of long-day plants and continuous darkness for short-day plants. The seeds are then sown in field. Since the treated seeds have already completed the first two developmental phases, they progress to flowering more rapidly than the untreated ones.

8. Vernalisation of some crops.—In bulletin No. 17 of the Imperial Bureau of plant genetics (1935) the results of vernalisation tests on crop plants in different countries are reported. At the Imperial Agricultural Research Institute, Pusa, chilling wheat seeds at 0°—4°*C* for 2 weeks showed no difference in maturity. In the case of barley, treatment for one week accelerated flowering by 4·42 and 0·11 days in respect of two varieties while treatment for two weeks retarded flowering by 2·49 and 11·92 days in the same varieties. In oats, treatment for 2 weeks accelerated flowering by ·669 and 1·48 days in the case of two varieties.

The Department of Agriculture, Nagpur, report that chilling *Sorghum* seeds at 10°*C* in darkness for 10 days showed acceleration of maturity by 4 days. The Millets Specialist at Coimbatore has tried the treatment on *Sorghum, Setaria italica, Eleusine coracana* and *Pennisetum typhoides*. No practical differences were noticeable. In the case of rice, at Coimbatore it was found that treatment at 10°—20°*C* in darkness for a period of 3 weeks showed acceleration of flowering by 4·8 days.

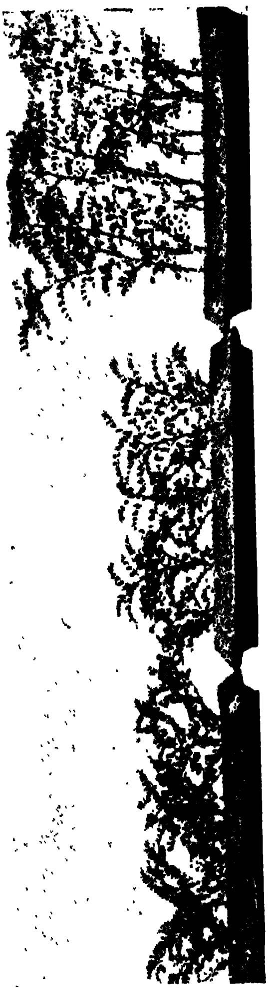


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Fig. 148.—Seeds of Bengal gram vernalised at 2°C and light treated. The plants under long-day treatment flowered while the plants with short-day and natural day length did not flower.

Fig. 149.—Plants under short days and natural days are in flowering stage, while plants under long days are in fruits.

Systematic and detailed investigations were carried out at the Imperial Agricultural Research Institute, Delhi, in the case of gram, wheat, chillies and soya beans (1942). The method adopted was to sterilise and soak the seeds for appropriate period under room temperature. Germinating seeds were then chilled at 2°*C* for varying periods and then sown. The seedlings in pot were then subjected to long-day (16 hours), normal day and short day (6 hours) conditions. The effect of treatment on flower initiation and fruit formation

TABLE 101.

Variety.	Treatment.	Effect of pre-sowing temperature treatment.				Effect of pre-sowing temperature treatment *plus* treatment after sowing.				
		Initiation of flower buds.		Opening of flowers.		Number of days taken for initiation of flower buds.			Acceleration in days over normal days due to	
		Number of days.	Accelera-tion in days.	Number of days.	Accelera-tion in days.	Long day after sowing.	Normal day after sowing.	Short day after sowing.	Long day.	Short day.
I.P. 9 ...	2°C for 26 days ..	78·30	15·46	89·36	13·22	45·00	64·70	65·80	19·70	—1·10
	Untreated	93·76	...	102·55	...	47·90	84·50	82·40	36·60	2·10
,, 17 ...	2 C for 26 days ..	84·63	6·93	94·85	4·14	...	...	...	...	...
	16 C for 16 days ...	93·41	—1·83	100·78	—1·8	...	...	...	...	...
	Untreated	91·58	...	98·98	...	...	...	...	...	...
,, 48 ...	2°C for 26 days ...	78·51	0·54	89·06	2·49	69·00	60·80	74·30	8·20	—5·30
	16°C for 16 days ...	83·51	—4·46	93·59	—2·04	..	...	...	...	...
	Untreated	79·05	...	91·55	...	62·10	78·30	82·50	16·20	—4·20
,, 70 ...	2 C for 26 days ..	81·90	—1·30	93·89	—1·24	...	...	...	...	...
	16°C for 16 days ...	81·30	—0·70	93·37	—0·72	...	...	...	...	...
	Untreated	80·60	...	92·65	...	...	...	...	...	...

— (*minus*) indicates delay in flowering.

were noted. The effect of pre-sowing temperature treatment on bud initiation and flower opening in gram is shown in Table 101. (Figs. 148 and 149).

The data show that in the case of two varieties only vernalisation at 2°*C* induced earlier flowering and the same treatment at 16°*C* delayed flowering. In either case, the effects were not sufficient enough to be of economic importance. Tests with the effect of light treatment alone on unvernalised seeds showed the effect to be more marked as shown in Table 102 :—

TABLE 102.

EFFECT OF LIGHT TREATMENT ON UNVERNALISED GRAM SEEDS.

Variety.	Light treatment after sowing.	Initiation of flower buds.		Opening of flowers.	
		Number of days.	Acceleration over normal days.	Number of days.	Acceleration over normal days.
I.P. 9 ...	Long day ...	47·38	29·62	54·57	32·38
	Normal day ...	70·00	...	86·95	...
	Short day ...	82·81	—5·81	91·36	—4·41
I.P. 48...	Long day ...	57·48	23·04	63·85	26·07
	Normal day ...	80·52	...	89·92	...
	Short day ...	76·92	3·6	84·35	5·57

In both the varieties long day condition accelerated flower formation.

In the case of experiment with wheat, (Fig. 150) English winter wheat showed that low temperature at early stages and long-day conditions during growth hastened maturity while the Indian wheat varieties were indifferent to temperature treatment. The effect of low temperature treatment on English wheats was more pronounced when the sowing was in spring and there was no effect when sown in winter in Simla.

In the case of reaction to light, the untreated seeds of Indian varieties matured earlier under long-day conditions. While the English varieties showed delay in flowering as shown in Table 103.

The treatment on chilly and soya-bean showed that it had negative or negligible effect. In the case of chilly, initial period of darkness immediately after sowing retarded flowering; continuous light had the same effect. Figs. 151 and 152 show the effects of vernalisation on linseed and mustard.

9. **Genetic conception.**—Lysenko's theory of phasic development introduces a new conception in regard to the genotype and phenotype. In the preceding chapters, Mendelian conceptions were presented and here Lysenko's interpretation is indicated. In sexually reproduced plants, the individual is a product of the fusion of two gametes which latter represent two genotypes. The individual is full of potentialities derived from the two parental lines. If these potentialities are to be made use of, they must run through the develop-

mental course and express themselves into phenotypes, and according to Lysenko this is possible under appropriate environment only. For example, in F_1 both the allelomorphic pairs of genetic factors are present and that allelomorph which finds the environment favourable to it will develop. Thus

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Fig. 150. English wheat winter sown. Vernalised for 35 days and exposed to long-day. Vernalised plants with control in the centre.

dominance-recessive phenomenon rests on environment and the adaptability of the zygote in its biological development. *Lysenko* (1937) *is of opinion that hereditary characters may be changed in ontogenesis by environment.* Instead of individual factors, the entire germ cell is taken as the hereditary basis. Genotype of cereals can be changed in the desired direction by growing the plants in a specially selected environment. Lysenko speaks of " *training* " the plants, a process by which the plants can be gradually changed from one form to another and these changes are transmitted to the progenies. It will be seen that many of the genetic conceptions presented here are at variance with those expressed in the preceding chapters. At present, greater details of the experiments of Lysenko are not generally known outside Russia.

In regard to the value of vernalisation to a breeder, Lysenko takes it as a complementary step in breeding programmes. The central theme of vernalisation is that, developmental processes may be induced in a germinating seed and not necessarily in a grown-up plant. The vernalised seed, though for external purposes may appear as seed, is to be regarded as a seedling.

TABLE 103.

EFFECT OF LIGHT TREATMENT ON THE EARING OF PLANTS FROM UNVERNALISED SEEDS.

Variety.	Light treatment after sowing.	Number of days taken for first bloom.	Acceleration in days over normal.
English ...	Long day for 31 days	165·14	—14·74
Wheat ...	Long day for 63 days	No flowering.	...
Yeoman III ...	Short day for 32 days + long day for 32 days.	161·90	—11·50
	Short day for 32 days + normal days ...	154·90	—4·50
	Short day for 54 days followed by normal days.	156·40	—6·00
	Normal days throughout	150·40	...
I.P. 114 ...	Long day for 54 days	45·96	44·11
	Long day for 31 days	47·26	42·81
	Long day for 31 days followed by short day for 23 days.	51·32	38·75
	Short day for 32 days followed by long day for 22 days.	74·76	15·31
	Normal day throughout	90·07	...
	Short day for 32 days	100·69	—10·62
	Short day for 54 days	108·44	—18·37

In treated seed the embryo is prepared for sexual reproduction and the latter is separated in time from growth. In practical application, the process has been adopted in Russia in growing superior varieties in a locality where

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Fig. 151. Linseed Pusa 12 Vernalised for 1 month (Marked V). The vernalised plants were early by 60—75 days.

normally the variety does not flower and set seed. The process is also applied to make the variety to flower earlier and thus escape damage by heat or frost.

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Fig. 152. Mustard T. 27 Vernalised for 6 weeks (Marked V).

In Ukraine, where late maturing spring wheats are damaged by heat, vernalisation was adopted to make the plants head earlier. The results are presented in Table 104.

TABLE 104.

Variety.	Sowing.	Ear formation.	Accelera- tion (—) retarda- tion (+) in days over Girka.	Yield as % over Girka.
(1) Azerbaijan : *Erythrospermum* 534/1 :				
Vernalised ...	11—4 –1931	5th June	—9	111·7
Untreated ...	,,	1st July	+ 17	4·7
(2) Azerbaijan : *ferrugineum* :				
1316/8 : vernalised ...	,,	12th June	– 2	141·1
untreated ...	,,	1st July	+ 17	7·9
(3) Odessa Girka 0274 milturum ...	,,	14th July	0	100

The first two varieties which were unsuited to Odessa conditions have given increased yields over the superior local type when the seeds were vernalised and sown. Thus, vernalisation is helpful in introducing foreign types which do not normally flower in the new place.

Chapter 22

CROP DETERIORATION

SEED PURITY—MECHANICAL ADMIXTURE—ROGUING—GENETIC CAUSES FOR DETERIORATION

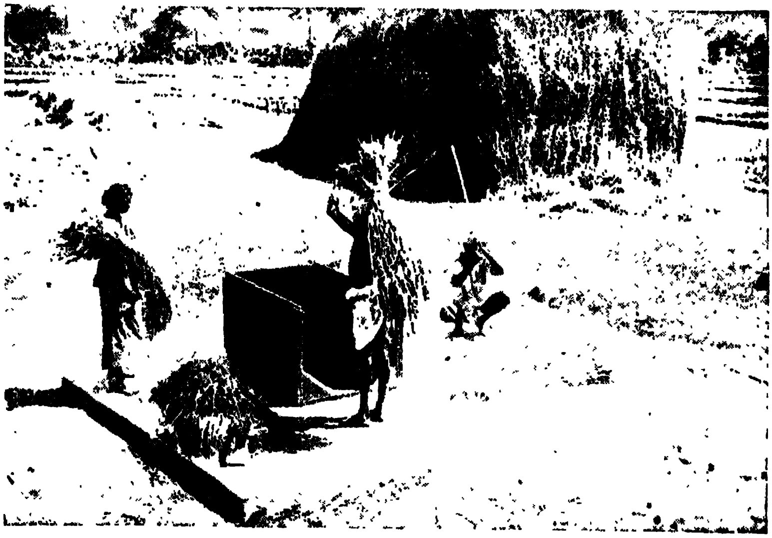
1. **Seed purity.**—It has been pointed out in earlier chapters that in naturally existing populations the individuals that constitute the population may differ from one another in a smaller or larger degree. In other words, the naturally existing population shows variability. This variability is greater in the case of crops which are cross-pollinated. The breeder selects the most favourable genotype and issues it to the ryots as an improved strain. In the case of mass selection, the seeds of desirable plants are mixed together and the uneconomic types in the bulk are eliminated. This raises the mean value of the characters for which selection is made by the breeder. In the case of pure-line selection, the most desirable individual plant is selected and its progenies are further selected for the purity in the characters under selection. Homozygosity of the population is aimed at.

It is now known that even under rigorous experimental conditions, the attainment of homozygosity to the theoretical standard is next to impossibility, as the material always retains some potentiality for genotype change. It has been shown that a homozygous type that perfectly fits into the existing environment may be altogether eliminated when the environment changes. In the case of cultivated crops, there are various ways by which the environment may change. The extension of cultivation of a particular crop may necessitate its being raised in varying soil and climate : the cultural practices may vary. All these have a bearing on the performance of the crop. The breeder's aim is to evolve a type that behaves uniformly under varying conditions. For example, G.E.B. 24 rice strain of Coimbatore gives excellent yield and maintains its fine quality under varying agricultural conditions of the Madras Province.

It was mentioned that the attainment of homozygosity even in self-fertilised crops is difficult. It is much more so in respect of cross-fertilised crops or hybrid progenies. The greater the differences between the parents that enter the cross, the greater is the instability of the hybrids and the balancing of genotypes takes longer time. In the case of polygenes, Mather (1941) pointed out that in homozygous types *internal balancing* and in heterozygous types *relational balancing* throw out variations. It has been pointed out that perfectly homozygous types are disadvantageous under natural conditions. The environment has two-fold effect on the individual. Firstly, it has directional effect in respect of certain characters and the failure of the plant to adapt itself will lead to its extermination. Secondly, environment causes fluctuations which have no significance in adaptation. There are two opposing tendencies in Nature (1) the one that necessitates the immediate adaptation of the individual to the existing environment and (2) the other, the necessity for variation at the cost of immediate fitness so that there may be advantage

in long-term selection. According to Mather, a compensating mechanism in the form of balanced polygenes exists in nature.

Naturally-existing bulk has been subjected to natural selection pressure over long periods and as such, is in a state of equilibrium even though it be heterozygous or heterogeneous. The improved strains issued by plant breeders are comparatively of recent origin and their composition has not been under natural selection for any appreciable period. Therefore, when the improved strain is released for spreading in the tract there are possibilities for natural selection to act differently on the population under different environment. Further, by open pollination with inferior local types, new hybrids may arise which will cause new variations to arise. All these factors contribute to what is generally termed as "*deterioration*" or "*running out*" of improved strains. Both the breeder and the ryot must take certain steps to prevent this happening or at least to slow down this process. This problem is discussed in this chapter.



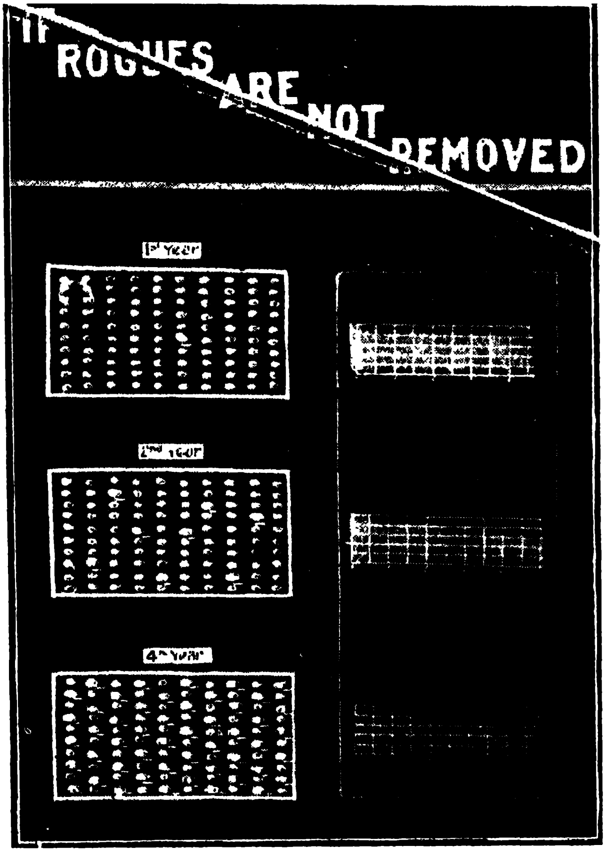
(*Photo from Paddy Specialist.*)

Fig. 153. A wooden box is used to prevent shattering and admixture of seeds during threshing.

2. Mechanical admixture.—One of the potent causes that lead to rapid deterioration is the seed impurity due to mechanical admixture. This generally happens due to careless handling of the seed. It is advisable for the ryots to preserve seed for next season from the harvest of this season. If this is not done and if fresh seed is purchased every year in the local market or from uncertified seedsmen, the improved strains are soon lost. In the case of cotton, the admixture may take place in ginneries. In general, it may be stated that the seed admixture may happen at any one of the following stages :

(1) Storage. (2) Seed bed. (3) Planted field. (4) Threshing floor. (5) Market.

There are various methods adopted by the ryots for storing grains. The commonest ones are storage in gunny bags, in straw twists, in pots or in special types of cellars. For want of accommodation, different varieties are stored so near to each other as to permit at least a few grains of one lot falling into the other. The receptacles should be thoroughly cleaned to see that not even a single grain from previous storage is sticking to it.



(*Photo from Cotton Specialist.*)

Fig. 154. A single rogue of first season multiplies rapidly within 4 years and causes deterioration in crop quality. Note the rapid fall in lint quality in the fourth year. Rogues are marked by a dash.

When seed bed is raised in the field, where the same crop had been standing in the previous season, there is possibility for mixture. In such cases, where practicable, the nursery area must be a fresh plot. In the preparation of the seed bed, sufficient time must be allowed for the shattered seeds to germinate and these unwanted seedlings may be either pulled out or ploughed in. When seed beds of different ryots are adjacent or when different varieties are sown in adjacent seed beds, by scattering, the seeds may get mixed up at least in the border areas. Similarly, when water is drained from one plot to another it may carry the seeds and thus cause mechanical mixture. The various processes outlined here may take place in the planted field also.

During the harvest season, there will be great rush of work at the threshing floor. In this country, the ryots very rarely have paved threshing floors of their own. Threshing is carried out in community grounds or in floors temporarily prepared for the season. Different varieties are threshed in the same floor or very near each other. Mixture may take place due to scattering. At least when the seed lot for next season is threshed, precautions on the threshing floor (Fig. 153) must be taken to prevent seed mixture.

3. **Roguing.**—Foreign types which are found in a pure line are termed "*rogues*", and the removal of the same is termed *roguing*. Rogues appear due to mechanical admixture in the seed material or by natural cross-pollination. A population with very negligible number of rogues to start with, shows increasing percentage of inferior types within a short space of time (Fig. 154).

The rogues are generally identified by certain morphological features which distinguish them from the improved strains. The rogues may be distinct enough for easy identification or they may not be externally distinguishable. Breeders often experience difficulties in maintaining the types pure. There are two aspects of this problem. On one hand, the extension of cultivation to unsuitable areas results in the deterioration of quality and yield in the improved strain and there may not be any genetical deterioration ; and on the other, the genetical deterioration may be such that it may not be easy to identify the off-types.

In the case of Cambodia cotton of Coimbatore, an examination of the locally cultivated improved strain *Co.* 2 showed, that the complaints, that it has deteriorated by admixture with inferior types, was not true. There was wide general impression that Malvi cotton has seriously deteriorated due to influx of inferior seed from Nimar and Newar. A survey of the tract showed it to be baseless. There had been nearly twelvefold increase in area under this crop and the types spread to inferior lands. Here the amount and variability of inferior cotton increased. Therefore, the breeder faces the problem of selecting desirable types that will respond both in good and bad lands. The breeder must be constantly vigilant about the natural deterioration as well as satisfy himself that reports of deterioration coming from cultivators or traders are true to his knowledge. Deterioration of improved strains in the districts is often due to admixture with inferior types. This could be prevented by the various precautionary steps outlined in the preceding section.

It is not always possible to identify the off-type from the improved type. The basis may be genotypical without morphological differences. Love states that in Canada, difficulty was felt in maintaining Dauson's golden-chaff winter wheat pure. A number of off-types appeared and these were found to be due to loss of segments or whole chromosomes. Certain types, morphologically indistinguishable from the improved type, give rise to inferior progenies in future generations. By cytological and morphological examinations, these off-types were eliminated and pure-breeding types were maintained. In the case of Kanred wheat, resistance to rust is applied as a test for purity.

4. **Genetic causes of deterioration.**—The breeder must consider the following causes of deterioration. (1) Place effect or developmental variation, (2) Mendelian variation, (3) Mutation with large and perceptible effects or small and imperceptible effects, (4) Natural selection in which the pests and diseases may be the main factors, (5) Residual genetic variability of the selected strain.

Place effect or developmental variation was already discussed. The spread of the improved strain to lands not suited to it may result in lower yield and inferior products, as evidenced in the case of Malvi cottons.

Mendelian variations may arise due to stray natural crossing. Even in self-fertilised crops stray natural crossing takes place. Therefore in field bulks, where artificial protection against cross-pollination is not possible, in the third season, off-types may be noticed due to segregation in natural crosses. By suitable tests, these off-types are rogued out. In the Central Research Station, a seed nucleus plot must be maintained. The plants in this plot must be selfed and the selfed seeds are to be utilised for multiplication of the strain (Fig. 155).

Mutations with large effects can be identified and rogued out. Generally the mutation rate is so low that it is not likely to constitute any potential danger. Mutations with small and imperceptible effects are found to be many and they play important role in evolution (East 1935). These *micro-mutations* constitute a real danger but any deterioration due to such phenomena may be prevented by maintaining seed nucleus plot. In the case of vegetatively propagated plants, bud mutations, which yield inferior buds constitute a real danger. Sufficient care must be paid to select the proper bud for propagation. Only the best plants must be selected for propagation.

Natural selection operating against the breeder's trend of selection is one of the important causes for deterioration. In Chapter XII, this aspect was dealt with in detail. If the genotypes selected by the breeder are such that they are not suited to the environment, some of them may be eliminated rapidly in nature. That genotype which is best suited to the environment multiplies rapidly. Selections of hybrid progenies do retain certain amount of genetic variation due to heterozygosity which it is difficult to eliminate without selfing the plants over a series of years. Natural selection may operate on this residual variability and as a result, inferior types may multiply. Reference was already made to physiological forms in the pests and diseases. Selection of strains resistant to all physiological forms of pests and diseases is an impossible task. In the case of wheat rust survey it was found that the relative spread of the physiological forms varies every year. New physiological forms may arise and the once-resistant strain may succumb to these. The failure of Co. 213 sugarcane in North India is attributed to a lighter strain of recent origin in *Colletotrichum falcatum*. The sudden failure of P.O.J. 213 in Louisiana is attributed to the increase in lighter race of this fungus. The variety is resistant to the darker race, but susceptible to the lighter race. Since the sugarcane variety was resistant to the darker race of the fungus, the latter could not multiply in nature. This gave an opportunity to the lighter race of fungus to multiply rapidly and cause damage to the crop. These examples

indicate that *the "deterioration" of a variety may not in fact be attributable to genotypic changes in the crop plant but to evolutionary tendencies in the natural enemies of these plants.* The breeder can overcome the problem by a continuous programme of breeding for resistance even to the newer races of pathogens.

(*Photo from Cotton Specialist.*)

Fig. 155. Selfing in Cotton. The flower marked by a circle is 'selfed' by smearing potter's clay round the petals to prevent their opening out.

The fifth cause of deterioration referred to above is the genetic variability of the material. In dealing with the selection of pure lines it was pointed out that it is next to impossibility to secure a perfectly homozygous type and that depending upon the field technique in selection, variability may still be observed in the selected types. This defect will be less in the case of normally self-pollinated crops than in the case of selections from hybrid progenies. A case of the latter type is reported from Bombay where a synthetic strain of rice was released for large scale cultivation without the necessary tests at the Breeding Station. Under large scale cultivation the complex heterozygotes threw out inferior and varying types that caused segregation. Especially

in the case of disease resistance where the pathogens may show a large number of physiological races, such deteriorations are frequent due to the sudden multiplication of pathogenic forms which under normal circumstances are not widely spread. Therefore, in the case of breeding for disease resistance it is essential to test the strain for homozygosity for resistance under controlled optimum conditions of infection. Field tests are not sufficient for the purpose.

5. **Prevention.**—Since mechanical admixture of inferior types of seeds with the improved strain is the frequent cause for deterioration, the ryots must take all steps to prevent such admixture. Roguing must be practised on large scale. It is advisable for the ryots to renew their sowing seeds at least once in five years and get sowing material from agricultural farms or certified seedsmen. The extension of cultivation of the strain to areas not suited for its cultivation must be avoided.

The Research Stations must maintain seed multiplication plots wherein the purity of the strain must be under test every year. This may be done by selecting single plants every year and testing a large number of them for homogeneity. If they all prove homogeneous, the bulk from such a lot is multiplied and seeds sent to districts for distribution.

If the deterioration of strain is really due to genetic causes *secondary selection* is practised to evolve a better strain.

STATISTICS

Chapter 23

STATISTICS IN RELATION TO PLANT BREEDING

INTRODUCTION—SAMPLING—STATISTICAL CONS NTS—TESTS OF SIGNIFICANCE—CHI—SQUARE

1. **Introduction.**—In the study of biological objects, the geneticist and the plant breeder have to deal with living objects, the nature of whose life characteristics exhibit fluctuations due to heredity or environment. On the other hand, the physical characteristics of mineral elements or compounds, such as the atomic weight of an element or the melting point or specific heat of a metal, do not exhibit such fluctuations. To correctly describe the biological objects or to compare two or more groups of biological objects, it is necessary to use certain methods of mathematical analysis. Since the characteristics of biological objects are variable, there is every possibility for personal bias and guess work on the part of the experimenter in drawing conclusions. Statistical analysis of data provide safe methods for drawing logical conclusions. The statistical methods are helpful (1) to design experiments (2) to reduce mass of data to simpler forms of descriptive statistics (3) to test the significance of observed effects.

2. **Sampling.**—If any character of a living population is to be studied, it will not always be possible to measure the variations found in all the individuals of the population due to limitations of time and energy. In such cases, it will be sufficient to study representative samples from such populations. If the technique of sampling is correct, conclusions from the data so collected will be valid even for the entire population. Any sample drawn from a population should be truly representative. For this purpose (1) *the sample must be of proper size in relation to the total population* (2) *every individual of the population must have an equal chance for inclusion in the sample* (3) *the population from which sample is drawn must not be varying under similar conditions.*

The samples may be drawn at random or at regular intervals. In random sampling, every individual of the population has equal chance with others for representation in the sample. In the case of sampling by design, samples at regular intervals are taken. *e.g.*, in a row of plants every *n*th plant may be taken into the sample ; or one plant for every *n* feet may be selected. If the population to be sampled consists of different types of plants, *i.e.*, if the population is *heterogeneous*, then every type must be represented in the sample.

The sample must be such that, conclusions drawn from different sets of samples from the same population must not differ widely. The conclusions drawn from different sets of samples from the same population in respect of any character must be close to one another. If they differ widely, it may be due to wrong technique in sampling, or unrepresentative nature of the sample due to its small size, or due to the high variations or heterogeneity of the population. It is important that the sampling technique must be sound and the samples must be large enough to give reliable data about the population.

3. **Statistical Constants.**—In the mathematical analysis of characteristics of the population through samples, certain *statistical constants* are used. Such constants help to describe the characteristics with precision and definiteness. The following are some of the important ones.

(i) *Arithmetical mean.*—A single value which stands for a number of measurements and which is constant for that sample is termed the arithmetical *average* or *mean. The sum total of all the individual measurements divided by their number yields the mean.* Table 105 shows 24 measurements of height of rice plants.

TABLE 105.

Serial Number.	Height in Inches.	Serial Number.	Height in Inches.
1	22	13	24
2	24	14	26
3	26	15	24
4	22	16	26
5	26	17	26
6	24	18	24
7	22	19	26
8	26	20	28
9	22	21	24
10	26	22	26
11	24	23	26
12	24	24	24
			Total ... 592

$$\text{Mean} = \frac{592}{24} = 24{\cdot}7''.$$

The 24 measurements presented in the foregoing table may be classified as shown in Table 106.

TABLE 106.

Frequency distribution.

Height of Plants in inches.	Number of Plants in each class.
20	0
22	4
24	9
26	10
28	1
30	0

The foregoing table shows how the frequencies of heights of plants are distributed. Each measurement is termed a *variate* and is the measured value of the *variable*, viz., the height. When large number of measurements of height is recorded, the data are unwieldy and so they are classified. In table 105, the height of plants varies from 22″ to 28″. This is termed the *range*. The range is then divided into convenient *classes* such as 22″, 24″, 26″, 28″. The number of individuals falling in any one class is the *frequency* of the class. When there are a large number of measurements and if the measurements are continuous, the class value is the mid-point of the class range. For example, if in a population of rice plants, height ranges from 21″ to 60″, the range may be divided

into convenient number of classes such as 21″—25″, 26″—30″, 31″—35″, 36″—40″, 41″—45″, 46″—50″, 51″—55″, 56″—60″. The class range is 21″—25″ and the class value is its mid-point 23″.

When the measurements are classified and presented in frequency distribution table, calculation of mean is easy. Each class value v is multiplied by its frequency f and the sum total (Σ) is divided by the total number of readings n. The mean M is therefore expressed by the formula.

$$M = \frac{\Sigma (v. f)}{n.}$$

When the individual readings are dispersed symmetrically around the mean, the graph in which the frequencies are plotted against their class values is unimodal (Fig. 156) with a single peak and bell shape. Such a curve is termed *normal curve*. From the figure it will be clear that the distribution of values on either side of the mean is equal. The peak of the curve representing the highest frequency is termed the *mode*. When the distribution is normal, the mean and the mode coincide.

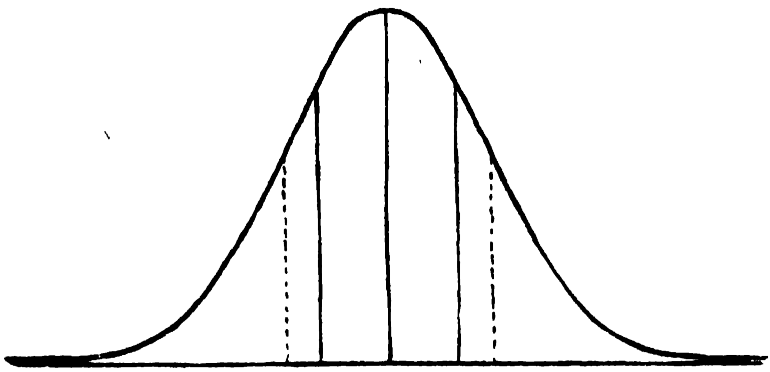


Fig. 156 Normal curve.

There are instances where the values are not symmetrically dispersed around the mean. The frequencies of such distribution when plotted in a graph exhibit *skew* form. In such cases, the mean and the mode do not coincide as in a normal curve.

(ii) *Standard deviation.*—The dispersion of the individual readings around the mean indicates the extent of variation in the sample and the measure of this dispersion, is determined by a statistical constant termed *standard deviation* (S. D. or σ). It is the square root of *variance*, the latter being the sum of squares (*s.s.*) of deviations (*d*) of individual readings from the mean *divided* by the number of degrees of freedom (D. F.$=n-1$) where n represents the number of readings. The formula for calculating S. D. may be expressed as follows :—

$$\text{S. D.} = \sqrt{\frac{\Sigma f. d^2}{n-1}}$$

The calculation of mean and standard deviation for the data presented in table 105, is shown below :

TABLE 107.

CALCULATION OF STANDARD DEVIATION.

Class value v.	Frequency f.	Assumed mean (A.M.).	Deviation from A.M. d.	$f.d.$	$f.d.^2$
22 ...	4	...	—4	—16	64
24 ...	9	...	—2	—18	36
26 ...	10	26·0	0	0	0
28 ...	1	...	+2	2	4
Total ...	24	...	...	—32	104

$$\text{Actual mean M} = \text{A. M} + \frac{\text{f.d}}{\text{n}}$$

$$= 26 + \frac{-32}{24}$$

$$= 24{\cdot}7''$$

$$\text{Standard Deviation} = \sqrt{\frac{fd^2 - \frac{(\Sigma fd)^2}{n}}{n-1}}$$

$$= \sqrt{\frac{104 - \frac{-32^2}{24}}{24-1}}$$

$$= 1{\cdot}63.$$

The deviations in column 4 of table 107 may be worked out from the actual mean 24·7. To facilitate ease in calculation, 26·0 is assumed as mean and the correction factor $\frac{fd}{n}$ is added to it to get the actual mean. In calculating the S. D. a similar correction factor is applied.

The standard deviation 1·63 is a measure of dispersion of the 24 measurements around the mean 24·7". When it is expressed as percentage of the mean, it is termed *co-efficient of variability* (C. V.) and it is expressed by the formula :

$$\text{C. V.} \quad = \frac{\text{S. D.} \times 100}{\text{M}}$$

$$= \frac{1{\cdot}63 \times 100}{24{\cdot}7}$$

$$= 6{\cdot}6\%$$

This is useful in comparing the variability or standard deviations of sets of measurements recorded in different units or having means differing in magnitude.

(iii) *Standard Error.*—Instead of a single sample, if more samples are drawn from a population and the standard deviation for each mean is calculated, it will be seen that the different values of standard deviations will be varying. The mean from different samples drawn from the same population must be the same or very close to one another so that a single sample may be reliable as a true measure of the population. A statistical constant which measures the dispersion of the means is termed *standard error* (S. E.), and is calculated by dividing standard deviation by $\sqrt{n}$. The formula may be expressed as follows :—

$$\text{S. E.} = \frac{\text{S. D.}}{\sqrt{n}}$$

$$= \frac{1{\cdot}63}{\sqrt{24}}$$

$$= 0{\cdot}326.$$

While standard deviation is a measure of the dispersion of the variables around the mean, standard error is a measure of the dispersion of the mean around the grand mean.

4. **Tests of Significance.**—It is often found necessary to compare two or more populations with regard to their measurable characters. In order to determine how far their mean values are different from one another, the extent of chance variations present in the samples is made use of as an index. For example, if the difference between means is very narrow indicating that the samples are from the same population, it would mean that if the measurement; are repeated there is no guarantee of the differences being maintained. In other words, the observed differences should be described as due to chance and not to inherent variations. In biological and agricultural experiments, the degree of accuracy required is usually of the order of 5% probability. In other words, the difference between means is said to be reliable or *significant* if it should occur in more than 5 trials out of 100. *Any observed difference between means is tested for significance by dividing it by the standard error of the experiment which gives the value of ' t '.* The theoretical values of *t* at 5% are calculated and given in tables by Fisher (*vide* appendix I). By reference to Fisher's table the significance or otherwise of the difference may be concluded. If the observed value of *t* from the experiment is lower than that given in Fisher's table for 5% level, the difference is said to be *not significant* or *vice versa.*

The following illustrates the method of testing the significance of the difference between two means.

TABLE 108.

LINT LENGTH IN TWO COTTON STRAINS A & B.

Number of readings.	Lint length in mm. Strain A.	Strain B
1	22	25
2	24	24
3	20	26
4	19	27
5	21	25
6	23	28
7	24	24
8	21	26
9	20	25
10	22	25
Mean	21·6	25·5
S.D.	1·71	1·27
S.E.	$\frac{1\cdot71}{\sqrt{10}}$	$\frac{1\cdot27}{\sqrt{10}}$
	$=0\cdot541$	$0\cdot402$

$$S.\ E._{D} = \sqrt{0\cdot541^2 + 0\cdot402^2}$$
$$= 0\cdot675.$$

Any difference between the two means greater than $2 \times 0\cdot675$ or $1\cdot350$ is significant and any difference less than $1\cdot350$ is due to chance errors in sampling. In small samples where the degrees of freedom do not exceed 30, $\frac{\text{difference}}{S.E._{D}}$ calculated from the data, should exceed the value of t from Fisher's table.

In the example,

$$\frac{D}{S.E._{D}} = \frac{3\cdot9}{0\cdot675}$$
$$= 5\cdot78$$

From Fisher's table, for 18 degrees of freedom at 5% level, the value of t is 2·101 which is much less than 5·78. Therefore, the observed difference between the two samples A and B is significant.

5. **Chi-square (χ^2) test.**—The statistical methods discussed so far, refer to sampling in a population and to distinguish chance variations in the sample. In the case of genetic experiments, the problem is to find out how far the observed data agree with the expected one.

Example 1.—In a cross between early and late types in rice, 3471 early types and 1199 late types appeared in segregating families. On the assumption that the character pair early—late is governed by a single pair of Mendelian allelomorphs, in the total population of 3471+1199 or 4670, there should have appeared 3502·5 earlies and 1167·5 lates (on 3 : 1 ratio with earliness as dominant

over lateness). It is seen that the data from the field are not the same as the expected ones. It is to be considered as to how far, the deviation (*d*) from the expected (E) is due to chance. Chi-square (χ^2) test is applied to determine the *goodness of fit* between the observed and the expected data.

TABLE 109.

	Early	Late
Observed	3471	1199
Expected	3502·5	1167·5
Deviation	31·5	31·5

$$\chi^2 = \Sigma\left(\frac{d^2}{E}\right) \quad \chi^2 = \Sigma\left(\frac{d^2}{E}\right)$$

$$\frac{31 \cdot 5^2}{3502 \cdot 5} + \frac{31 \cdot 5^2}{1167 \cdot 5}$$

$$= 1 \cdot 13.$$

The segregation is into two classes, *viz.*, early and late, and the degrees of freedom (D. F.) is 1. (D. F.=classes of phenotypes in the segregating families minus one). By referring to χ^2 table (*vide* appendix II) for $n = 1$, and $P = 0{\cdot}05$, the value is 3·841. When the value of χ^2 from table is greater than the value calculated from the experimental data, the assumption that the segregation is on 3 : 1 basis is taken as correct. In other words, the deviation of the observed from the expected is due to chance error.

Example 2.—In rice, E. B. 141 is a type with long outer glumes and T. 1083 with ordinary short outer glumes. In the cross E. B. 141 × T. 1083, the F_1 showed intermediate type of outer glumes and in F_2, the following data were obtained.

TABLE 110.

——	Ordinary outer glume.	Inter-mediate type.	Long outer glume.
Observed	436	808	412
Calculated on 1 : 2 : 1 ratio ...	414	828	414
Deviation ...	22	20	2

$$\chi^2 = \frac{22^2}{414} + \frac{20^2}{828} + \frac{2^2}{414}$$

$$= 1 \cdot 66.$$

There are three classes of phenotypes on segregation, DF=2, and the value of χ^2 for $P = 0{\cdot}05$ from table (*vide* Appendix II) is 5·991. The segregation is therefore on 1 : 2 : 1 ratio and the deviation of the observed from the expected is due to chance.

Example 3.—The cross between *Kafir* and *milo Sorghum*, discussed in Chapter III is taken here as an example. The frequencies of the four phenotypes which appeared on segregation are presented in Table 111.

TABLE 111.

	Umbonate Shape-Pink Colour.	Umbonate Shape-White Colour.	Round Shape-Pink Colour.	Round Shape-White Colour.
Observed frequencies ...	279	79	116	29
Expected frequencies on 9 : 3 : 3 : 1 ratio ...	283·0	94·3	94·3	31·4
Deviation ...	4·0	—15·3	21·7	2·4

$$\chi^2 = \frac{4{\cdot}0^2}{283{\cdot}0} + \frac{-15{\cdot}3^2}{94{\cdot}3} + \frac{21{\cdot}7^2}{94{\cdot}3} + \frac{2{\cdot}4^2}{31{\cdot}4}$$
$$= 7{\cdot}71.$$

The value of χ^2 from tables at P=0·05 and D.F.=3 is 7·815. This is greater than the value of χ^2 from the experiment. Therefore the assumption that the segregation is on 9 : 3 : 3 : 1 ratio is correct. The observed deviations are due to chance and hence *not significant.*

Chapter 24

CORRELATION AND REGRESSION

1. **Correlation.**—We have seen that in the study of attributes of biological objects, a certain amount of variation is present, the magnitude of which could be estimated in terms of certain statistical constants like standard deviation and standard error. There are other cases where two different attributes of the same population may exhibit certain relationship in their variability. In other words, the variation of one attribute is positively or negatively related to the variation of the other attribute. Such a relationship is termed *Correlation*. For example, heights of plants may be positively correlated to number of internodes or length of internodes ; yield may be correlated to the number of tillers in rice plant. Therefore the importance of the study of such relationship in biological material is great indeed. A measure of the amount of relationship between two characters is indicated by *co-efficient of correlation*, which may be positive or negative. *When the correlation is complete, whether it may be positive or negative the co-efficient of correlation is then* $\pm$ 1·0. *The co-efficient of correlation from the data of any two variables can never exceed unity.*

The following is the procedure to calculate co-efficient o correlation of characters which are correlated.

The data of measurements of two characters are formed into a two-way table in which the frequencies of occurrence in various classes of the two attributes are entered. The data pertaining to plant height and flowering duration in rice are presented in table 112.

TABLE 112.

Flowering frequencies.

Height frequencies.	83—86	87—90	91—94	95—98	99—102	103—106	107—110	111—114	115—118	119—122	123—126	Total.
35—38	4	6	5	4	2	2	...	...	...	...	...	23
39—42	9	26	25	21	18	8	3	...	...	...	...	103
43—46	5	35	48	60	54	27	9	2	2	2	...	244
47—50	3	12	53	80	91	71	31	13	5	2	...	361
51—54	...	2	17	31	75	108	54	47	16	10	4	364
55—58	...	1	4	7	15	36	37	36	25	12	1	174
59—62	...	...	...	1	2	9	21	39	32	16	3	123
63—66	...	...	...	...	...	2	5	12	4	5	...	28
67—70	...	...	...	1	1	1	...	...	...	...	...	3
Total ...	21	82	152	205	251	264	160	149	84	47	8	1423

Correlation co-efficient r is given by the formula :

$$r_{xy} = \frac{\text{Covariance}_{xy}}{\sqrt{\text{variance}_x \times \text{variance}}}$$

where x and y represent the two variables. The computation of co-efficient of correlation is done by re-arranging the data as shown in table 113.

TABLE 113.

Height Y.							Flowering duration X.						
Height in inches Y Class-centre.	Deviation d.	Frequency f.	f. d.	f d².	Total for X. Tx.	Product Txy.	Flowering duration in days y Class-centre.	Deviation d.	Frequency f.	f d.	f d².	Total for y. Ty.	Product. Txy.
1	2	3	4	5	6	7	8	9	10	11	12	13	14
36·5	1	23	23	23	69	69	84·5	1	21	21	21	49	49
40·5	2	103	206	412	379	758	88·5	2	82	164	328	227	454
44·5	3	244	732	2.196	1.008	3,024	92·5	3	152	456	1.368	520	1,560
48·5	4	361	1.444	5.776	1,773	7,092	96·5	4	205	820	3,280	759	3,036
52·5	5	364	1,820	9,100	2,244	11.220	100·5	5	251	1,255	6,275	1,052	5,260
56·5	6	174	1.044	6.264	1,236	7,416	104·5	6	264	1.584	9,504	1,227	7,362
60·5	7	123	861	6,027	1,008	7,056	108·5	7	160	1,120	7,840	836	5,852
64·5	8	28	224	1,792	229	1,832	112·5	8	149	1,192	9,536	878	7,024
68·5	9	3	27	243	15	135	116·5	9	84	756	6,804	512	4,608
							120·5	10	47	470	4,700	288	2,880
							124·5	11	8	88	968	47	517
Total ...		1,423	6.381	31,833	7,961	38,602			1,423	7,926	50,624	6.395	38,602

$y = 50{\cdot}46$ $\quad$ $x = 102{\cdot}78$

$$r_{xy} = \frac{N\ \Sigma_{xy} - T_x\, T_y}{\sqrt{(N\ \Sigma_{x^2} - T_x^2)\ (N\ \Sigma_{y^2} - T_y^2)}}$$

$$= \frac{1423 \times 38602 - 6381 \times 7961}{\sqrt{(1423 \times 31833 - 6381^2)\ (1423 \times 50624 - 7926^2)}}$$

$$= 0{\cdot}64.$$

Computation :—(Table 113).

(1) To simplify calculations, deviations (d) from arbitrary origin are adopted for y and x as shown in columns 2 & 9.

(2) The figures in columns 4 & 11 are the products of frequency (f) and deviation (d).

e.g., in the case of y, $1 \times 23 = 23$.
$2 \times 103 = 206$ and so on.

in the case of x, $1 \times 21 = 21$.
$2 \times 82 = 164$ and so on.

(3) The figures in columns 5 & 12 are the products of frequency (f) and square of deviations :

e.g., in the case of y, $1^2 \times 23 = 23$.
$2^2 \times 103 = 412$ and so on.

in the case of x, $1^2 \times 21 = 21$.
$2^2 \times 82 = 328$ and so on.

(4) The figures in column 6 indicate the totals for x array (Tx) and figures in column 13 indicate the totals for y array (Ty). These figures are calculated from the correlation tables :—

(Table 112).

For example :

For x-array

$4 \times 1 = 4$
$6 \times 2 = 12$
$5 \times 3 = 15$
$4 \times 4 = 16$
$2 \times 5 = 10$
$2 \times 6 = 12$

69

and so on for the 9 x-arrays.

and so on for the 11 y-arrays.

For y-array

$4 \times 1 = 4$
$9 \times 2 = 18$
$5 \times 3 = 15$
$3 \times 4 = 12$

49

Taking the x-array, each individual frequency is multiplied by the corresponding deviation and the total for the whole row comes to 69. The figures in columns 7 & 14 are calculated by multiplying the total of each x-array (Tx) by the corresponding deviation of Y : *e.g.*, 69×1 : 379×2 and so on. The total of these figures yields the product (Txy).

The significance of the correlation co-efficient is tested by 't' test for small samples and standard error test for large samples.

When the sample is large, the standard error of r is given by

$$S.\ E_r = \frac{1 - r^2}{\sqrt{N - 1}}$$

For the observed correlation to be significant, $\frac{r}{S.\ E_r}$ must be more than 2·0. If it is less than 2·0, the observed correlation is likely to be due to chance.

When the sample is small, the above test is not applicable but Fisher's 't' test is applicable.

$$t = \frac{r\sqrt{N - 2}}{\sqrt{1 - r^2}}$$

where N refers to the number of pairs of observations. Applying the test of significance to the example worked out here,

$$S.\ Er = \frac{1 - 0{\cdot}64^2}{\sqrt{1423 - 1}} = 0{\cdot}016.$$

$$\frac{r}{S.\ Er} = \frac{0{\cdot}64}{0{\cdot}016} = 40{\cdot}0$$

Since $\frac{r}{S.\ Er}$ is greater than 2·0, the observed correlation is significant.

2. **Regression.**—The correlation co-efficient r measures the total relationship between the variables x and y. It only signifies that a change in one variate is followed by a change in the other as indicated by the correlation co-efficient r but it does not indicate what is the change in one variate for a unit change in the other. This relationship is termed *regression co-efficient* (*b*) and with the aid of this co-efficient it is possible to predict the values of x for the given values of y or *vice versa*. There are thus two regression co-efficients *viz.*, regression of x on y termed b_{xy} and regression of y on x termed b_{yx}. In the example considered under section 1 of this chapter, b will represent increase in height in inches in rice crop for an increase of 1 day in flowering duration.

Regression co-efficient may be calculated from the correlation table and its value is given by the formulæ :

$$b = \frac{\sum (xy) - \frac{T_x T_y}{N}}{\sum (x^2) - \frac{T_x^2}{N}}$$

$$= \frac{N \Sigma (xy) - T_x T_y}{N \Sigma (x^2) - T_x^2}$$

In the case of the example presented in table 112,

$$b_{yx} = \frac{1423 + 38602 - 6381 \times 7926}{1423 + 31833 - 6381^2} = 0{\cdot}95$$

With the aid of the regression co-efficient it is possible to predict the value of y for the known value of x, from the formula :

$$Y = \dot{y} + b_{yx} (x - \ddot{x}).$$

where,

Y = predicted value of y.

$\dot{y}$ = the mean value of y.

b_{xy} = regression of y on x.

H = mean of x.

By applying this formula, the predicted heights in inches are shown in table 114.

TABLE 114.

Flowering duration.	Height in inches.	
	Observed y.	Predicted y.
92·5	34·5	40·68
95·3	38·5	43·35
98·0	42·5	45·91
100·1	46·5	47·91
105·1	50·5	52·67
108·9	54·5	56·28
113·8	58·5	60·34

The significance of any observed value of linear regression co-efficient can best be tested by testing the corresponding correlation co-efficient.

Chapter 25

FIELD TRIALS

OBJECT OF FIELD TRIALS—SOIL HETEROGENEITY—CHOICE OF SITE—SIZE AND SHAPE OF PLOTS—VARIANTS—LAY OUT—REPLICATION AND RANDOMISATION—SOWING, PLANTING AND HARVESTING OF EXPERIMENTAL PLOTS—DURATION OF EXPERIMENT—RECORD OF DETAILS OF FIELD EXPERIMENT—PAIRED PLOTS—RANDOMISED BLOCK—LATIN SQUARE—SPLIT PLOT DESIGN—LATTICE DESIGN—CO-VARIANCE.

1. Object of field trials.—The biologists in general and the plant breeders in particular, are interested in the improvement of crop yields. Since crop production depends upon inherent and environmental factors, the breeder feels the need to assess the values of these factors in the materials he handles at every stage of improvement. For example, in the improvement of rice, the breeder is interested to find out how far the quality and quantity can be improved by the introduction of high yielding bio-types and the adoption of suitable cultural methods, such as irrigation, manuring, intercultivation, spacing, etc. Therefore it is obvious that the breeder requires suitable technique whereby he can collect reliable data to assess the inherent and environmental effects in the plant material. In this direction, perforce he has to study the performance of the individual plant material under field conditions. Under such conditions the reaction is dependent upon mainly the soil conditions that affect crop growth. Hence any variation in soil fertility, i.e., *soil heterogeneity* will be the chief source of error in such experiments. Unless suitable field technique, which will minimise and assess such errors, is adopted it will not be possible to correctly evaluate the intrinsic worth of the material or treatment.

2. Soil Heterogeneity.—Before an experiment is laid out, the experimenter has to study the uniformity or otherwise of the soil in which he proposes to conduct experiments. For this purpose, the field is usually cropped in bulk and later at the time of harvest, divided into a number of small units and their yields individually recorded. It will be possible by grouping of individual units having similar yield to mark the fertility gradient of the field. It will be also possible to find out suitable size of plots that will reduce variations due to soil heterogeneity. If yield or cultural tests are laid out, after such determination of soil heterogeneity, it will be possible to reduce experimental error to a minimum.

3. Choice of Site.—In the selection of land for the conduct of experiment, it is necessary to observe the following precautions :

(*a*) Type of land selected should be representative of the soil in the tract in which the results of experiments are proposed to be utilised.

(*b*) Slopy and patchy areas of the field should be avoided.

(*c*) Presence of trees or other objects that will affect crop growth are to be avoided.

(*d*) Sites exhibiting high soil heterogeneity should be avoided for the purpose.

(*e*) The site selected should have had uniform cropping and cultural treatments during previous seasons.

(*f*) The size of field to be selected will depend upon the size of individual plots, number of treatments and the number of replications.

4. **Size and shape of plots.**—Size of plot varies with the crop and the nature of experiments. By conducting uniformity trials, the optimum size for each crop should be determined. In determining the size and shape, the convenience of conducting agricultural operations will form an important point to consider. If the plots are of small size, working of implements for cultivation, sowing, etc., will be difficult. However, if sizes increased considerably, the experimental error will be exaggerated. The optimum size has to be determined for each case.

In practice it has been found that a square plot gave a lower experimental error than a long rectangular one. When the plots are long, the border effects, as also the effects of soil heterogeneity are increased. Small size of plots such as 1/500, 1/250, 1/125, 1/100 of an acre show high standard deviation in the case of cereals and hence the plot size should be at least 1/40 of an acre (=2·5 cents).

5. **Variant (Treatments).**—It was once considered that in all agricultural experiments, only one treatment should be under test in an experiment. Grouping of a number of treatments for simultaneous study in one experiment was not in favour. With improvements in field technique and statistical analyses, complex experiments are now in favour. The latter facilitate greater accuracy in that (1) where two or three simple experiments will be necessary, one complex experiment may be sufficient to test the treatments, (2) it is possible to test the interactions between the different treatments ; *e.g.*, if varieties and manures are studied, it can be tested whether all the varieties under study react to the different manurial treatments to the same extent. The strains evolved by a breeder may show differences due to manures, number of irrigations and cultural treatments and these can be tested by designing a complex experiment.

6. **Lay-out.**—Having selected the field, determined the size and shape of plots, as well as the number of treatments, it becomes necessary to lay-out the experiment in a manner that will reduce the error, increase efficiency and yield data for valid statistical analysis. Lay-out of experiments is determined primarily by the number of variants and secondarily by the nature of treatments, *e.g.*, when the variants are only two, the lay-out can be only of a restricted pattern. When two or more types of variants are involved in the experiment, the treatments are grouped in such a manner as to form main and sub-plots

thus facilitating easy handling. Statisticians have designed appropriate statistical methods for analysing the data from each type of lay-out. The following are some of the important types of lay-out :

(i) Paired plots.
(ii) Randomised block.
(iii) Latin square.
(iv) Split plot.
(v) Lattice design.

7. Replication and Randomisation.—The most important factor in the conduct of an experiment is what is known as *replication* of the treatments. As already described, the effect of treatments in experiment is subject to errors due to soil heterogeneity. Such errors are considerably reduced by repeating or replicating the variants a number of times, depending upon (i) magnitude of soil heterogeneity, (ii) size of experimental error, and (iii) availability of land.

As the replications are increased the experimental error gets reduced. But in practice, a certain optimum number requires to be fixed for each type of experiment. Another advantage of replication is that it reduces if possible, to evaluate the magnitude of what is known as *random error* or *chance error*.

With the increase of replications, the area of land occupied by the experiment increases and therefore the soil heterogeneity also adversely affects the results. Hence a valuable method of controlling this defect is by the adoption of a *control* along with the variants in each replication. Location of such controls helps to reduce the error while replication reduces the error as well as gives an estimate of such error. Therefore, in any well thought out experiment, the treatments must be replicated sufficiently with local controls. For valid estimation it is also important that the various treatments should be arranged in a randomised manner within each replication and such a replication with all the treatments including the control is termed a *block*.

Earlier experimenters always arranged the treatments in a systematic manner, *e.g.*, if there were four treatments, the arrangement was always of the pattern A B C D, A B C D, etc. Such an arrangement introduces a bias, *i.e.*, any treatment always occupying the same position with reference to others. On the other hand, if the four treatments were randomised, there was the possibility of the treatments occurring in different positions of soil fertility and also with reference to one another. Such a method has been found to reduce the experimental error.

The number of replications in an experiment will depend upon (*a*) number of treatments, (*b*) degree of accuracy required, and (*c*) availability of land. Ordinarily the number of replications should be such that the number of degrees of freedom for error is not below 10. In agricultural experiments, with 4—8 variants, the number of replications should not ordinarily be less than 5 or 6. An increase in the number of replications, increases the degree of accuracy of the experiment. Whenever the land available for experiment

is limited it would be desirable to decrease the plot size and increase the number of replications.

8. Sowing, planting and harvesting of experimental plots.—In the conduct of field experiments, the following precautions are necessary :

(*a*) Uniform preliminary preparation of the land is necessary.

(*b*) Seed rate to be adopted should be the same throughout the area so that the number of plants in each plot is approximately the same, as otherwise, differential stand will introduce error in the experiment.

(*c*) Errors due to differential sowing, planting or harvesting should be avoided.

In the harvest of experimental plots, it is necessary, to eliminate border effects by having a belt of outskirts all round so that the central portion alone is taken into account for experimental purposes.

9. Duration of experiment.—Climatic factors greatly influence the yield from a crop. Different varieties react differently to seasonal variations—some can withstand drought and some cannot. Therefore it is essential that the yield trials should be repeated over a number of seasons to eliminate variations due to seasonal factors. The experiments should be repeated at least for three years. In district trials, it is advantageous to conduct the trials in different localities representative of soil and climatic types. In experiments dealing with perennial crops, the duration must be longer to arrive at reliable conclusions.

10. Record of details for field experiments.—The following are some of the important details to be recorded in respect of each experiment :—

(i) Name of the experiment.

(ii) Crop, season and year.

(iii) Object of experiment.

(iv) Variants or treatments.

(v) Previous cropping, cultural treatments, manuring, etc.

(vi) Site selected—field No. or Survey No.

(vii) Type of lay-out.

(*a*) Number of replications.

(*b*) Total number of plots.

(viii) (*a*) Total area under experiment.

(*b*) Total area under each treatment.

(*c*) Nett area under each treatment (dimensions of plots and area to be given).

(*d*) Number of rows or beds under experiment.

(*e*) Number of plants per row.

(ix) Method of sowing :

(*a*) Seed rate.

(*b*) System of sowing.

(*c*) Distances between plants in the row and between rows.

(*d*) Date of sowing or transplanting.

(x) Agricultural operations :
- (*a*) Preparatory cultivation.
- (*b*) Manures and manuring.
- (*c*) Thinning and filling up gaps.
- (*d*) Intercultivation and weeding.
- (*e*) Irrigation.

(xi) Observations on crop growth :
- (*a*) Selection of rows, plants, etc., for observations.
- (*b*) Presence and effect of weeds, pests, diseases, etc.
- (*c*) Seasonal observation on crop growth.
  - (i) Excessive rain.
  - (ii) Drought.
  - (iii) Temperature variation.
- (*d*) Date of flowering.
- (*e*) Date of maturity.

(xii) Date of harvesting, threshing, etc.

(xiii) Plan of lay-out with yield.

(xiv) Tabulation of yield per plot.

11. Paired plots or Beaven's half-drill method.—When two treatments only are under test, they may be paired in such a way that no one treatment is always placed to only one side of the other. The lay-out follows the pattern A B B A where the treatment A is both to the right and left of B unlike in the pattern A B A B where the treatment A is always to the left side of B. The lay-out and analysis of yield data are shown in the following example:

BEAVEN'S HALF DRILL METHOD" OR
STUDENT'S "PAIRED METHOD" OF LAYOUT

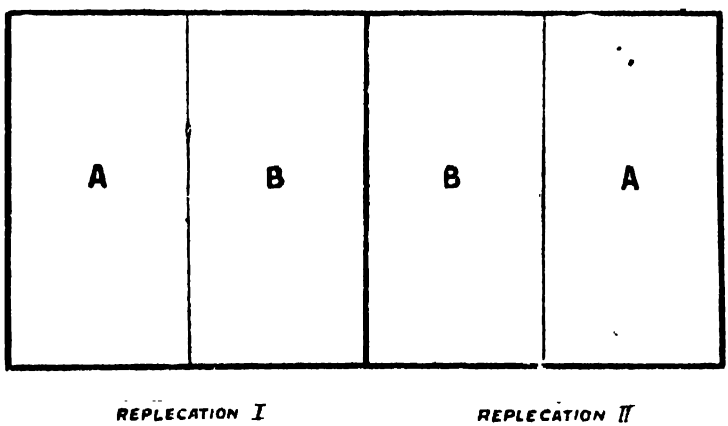


Fig. 157. Field Plan.

Two varieties A and B were tested for yield. Plan of lay-out is shown in figure 157. The method of analysis of yield data is shown on Table 115.

TABLE 115.

YIELD IN OZ. PER PLOT.

Replication.		A.	B.	A.B.	Deviation from mean. (d).	d^2.
1	...	33	22	11	7·4	54·76
2	...	23	34	—11	—14·6	213·16
3	...	19	28	—9	—12·6	158·76
4	...	29	27	2	—1·6	2·56
5	...	27	30	—3	—6·6	43·56
6	...	39	32	7	3·4	1·56
7	...	37	33	4	0·6	0·36
8	...	38	32	6	2·4	5·76
9	...	52	42	10	6·4	40·96
10	...	35	27	8	4·4	19·36
11	...	38	29	9	5·4	29·16
12	...	46	37	9	5·4	29·16
		416	373	43		609·12
Total	...	34·7	31·1	3·6		

$$\text{S. D.} = \sqrt{\frac{\Sigma d^2}{n-1}}$$

$$= \sqrt{\frac{609{\cdot}12}{12-1}}$$

$$= 7{\cdot}44$$

$$\text{S. E. of difference} = \frac{7{\cdot}44}{\sqrt{12}}$$

$$= 2{\cdot}15$$

$$t = \frac{\text{Mean difference}}{\text{S. E. of difference}}$$

$$= \frac{3{\cdot}6}{2{\cdot}15}$$

$$= 1{\cdot}67$$

t from table for P = 0·05, is 2·20. Since t calculated from experiment is less than t from Fisher's table, the results are *not significant*.

"Z" TEST:

$$\text{Students "Z"} = \frac{\text{Mean difference}}{\text{S. D.}}$$

$$t = \sqrt{}$$

∴ Value of 't' from experiment

$$= \frac{3{\cdot}6}{7{\cdot}44} \times \sqrt{12}$$

$$= 1{\cdot}67$$

12. Randomised Block.—As uniformity in soil conditions within a block is a primary consideration, number of varieties included in the test should be sufficiently small so that all varieties are almost under similar soil conditions. Hence it is advisable not to increase the number of plots beyond 10 in each block ordinarily, and under more uniform conditions upto 20. It is also desirable to have the block shape as square, as this will reduce the soil fertility differences within the block to the minimum. However in cases where tests with larger number of variants are necessary as in the case of progeny row tests, suitable reduction in the size of plots is adopted so that all variants in a replication are arranged within a compact block having almost uniform soil conditions.

In this type of lay-out, some measure of error control is obtained. The experimental field is divided into as many blocks of equal dimensions as it is desired to have replications. Each block should be as nearly a square as possible and this minimises error due to soil heterogeneity. Each block is then sub-divided into as many plots as there are treatments, all plots being of equal size. *In the case of end-plots, the size is increased to allow for marginal effects.* In each block or replication, each treatment occurs only once and its position in the block is decided by chance and not by any systematic arrangement. (Fig. 158).

Randomisation is carried out by taking a pack of cards, numbering them serially, shuffling and then drawing out cards. The treatments also are serially numbered. If there are 6 varieties to be tested, and the first card drawn bears the number 63, then 63 ÷ 5 gives remainder 3, and the third variety in the list is taken and placed in the first plot of the block. In this manner, the positions for 6 varieties are randomised in each block. This method of randomisation is slow and therefore Tippett's random sampling numbers may be used for ease and quickness.

The method known as *Analysis of variance* propounded by Dr. Fisher is adopted to test the significance of results. The great advantage of Fisher's method of analysis of variance over the older methods is that for evaluating the significance between the treatments, all the data are utilised in the derivation of standard deviation and standard error. This method provides for the elimination of block effect. It gives greater reliability of results as the number of observations or plot yields on which the constants are based are larger.

The plan of lay-out (Fig. 158) and analysis of variance are illustrated below :

Five Cambodia cotton selections were tested against standard for yield. The yield data are furnished in Table 116.

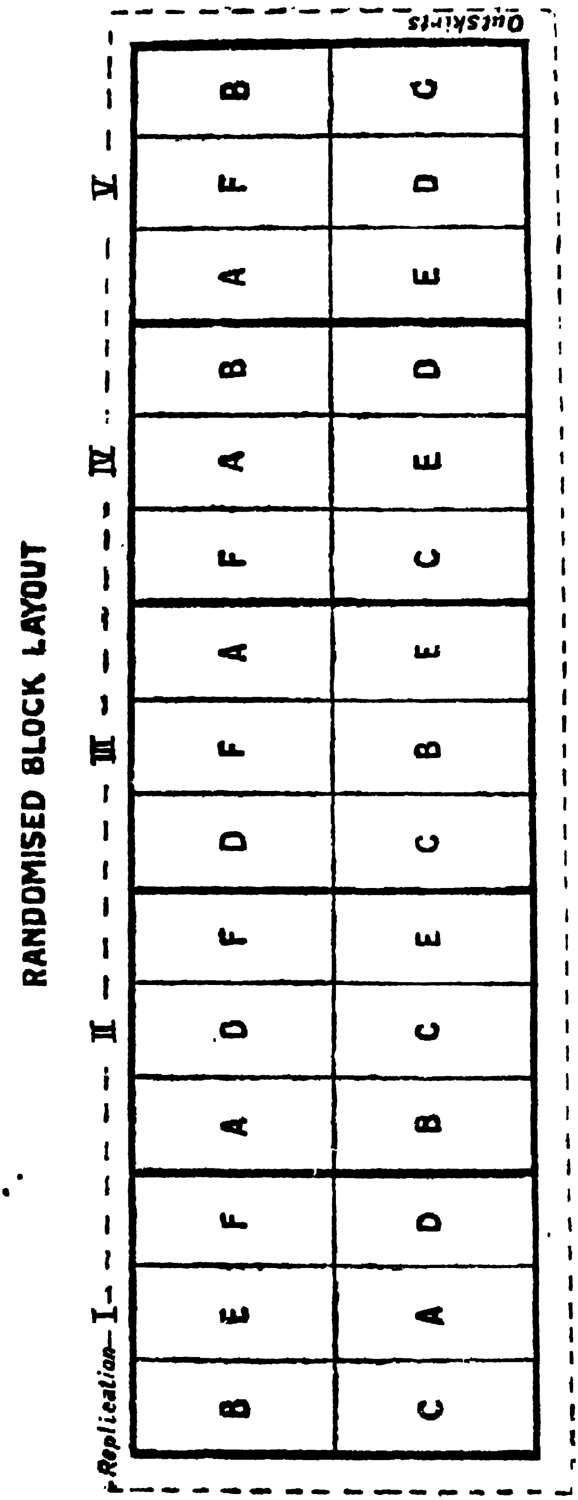


Fig. 158. Field plan.

TABLE 116.

YIELD (y).

(Wt. of seed cotton in ounce per plot.)

Culture.		Replication. I.	II.	III.	IV.	V.	Treatment Total.	Mean.
A	...	83	72	97	76	68	396	79·2
B	...	95	69	94	66	68	392	78·4
C	..	56	62	70	62	57	307	61·4
D	...	66	82	120	69	79	416	83·2
E	...	73	52	77	61	54	317	63·4
Standard F	...	58	65	55	62	53	293	58·6
Block total	...	431	402	513	396	379	2,121	

$$\text{General mean} = \frac{2121}{30}$$

7·07

$$\text{Correction factor} \quad \frac{2121^2}{30}$$

1,49,954·7

There are 30 plots in the experiment *viz.*, 6 varieties in each of the 5 replications. The 30 readings are squared and summed up.

TABLE 117.

SUM OF SQUARES (S.S.).

Culture.		Replication. I.	II.	III.	IV.	V.	Total.
A	...	6,889	5,184	9,409	5,776	4,624	31,882
B	...	9,025	4,761	8,836	4,356	4,624	31,602
C	...	3,136	3,844	4,900	3,844	3,249,	18,973
D	...	4,356	6,724	14,400	4,761	6,241	36,482
E	...	5,329	2,704	5,929	3,721	2,916	20,599
Standard F	...	3,364	4,225	3,025	3,844	2,809	17,267
		32,099	27,442	46,499	26,302	24,463	1,56,805

Total SS =156805—149954·7

=6850·3

S. S. for Treatment.	S. S. for Blocks.
1,56,816	1,85,761
1,53,664	1,61,604
94,249	2,63,169
1,73,056	1,56,816
1,00,489	1,43,641
85,849	
	9,10,991
7,64,123	

S. S. for Treatment :

$$= \frac{764123}{5} - 149954{\cdot}7$$

$$= 2869{\cdot}9$$

S. S. for Block :

$$= \frac{910991}{6} - 149954{\cdot}7$$

$$= 1877{\cdot}1$$

To estimate the variance in the experiment, the deviations of individual plot yields from general mean have to be computed. This may be done by (i) working with the actual mean or (ii) an assumed mean with correction factor.

The correction factor is given by the formula.

$\frac{[\Sigma(x)]^2}{n}$ where the assumed mean is zero.

$$= \frac{2121^2}{30}$$

$$= 149954{\cdot}7$$

Total S. S. is derived from the total of 30 squares in table 117 by applying the correction factor :

$$156805 - 149954{\cdot}7$$

$$= 6850{\cdot}3$$

S. S. for treatment is calculated by summing up the squares of total yield for 5 replications, *i.e.*, $396^2 + 392^2$ . . . . 293^2. Each treatment total is from 5 plots. Therefore the total of squares is divided by 5 and the correction factor applied to arrive at the variance per plot.

S. S. for blocks is calculated by summing up the squares of the total yield from the 6 varieties in each block *i.e.*, $431^2 + 402^2$ . . . . 379^2. Since the total for each block is from 6 varieties, it is divided by 6 and correction factor applied to arrive at the variance per plot.

Total variability or variance in the plot yields is expressed as the sum of squares of the deviations of all individual plots from the general mean of the experiment. The sum of squares thus obtained is apportioned to the known sources of variation as follows :—

(1) *due to blocks.*

(2) *due to treatments.*

(3) *due to random or uncontrollable causes in the experiment which furnishes the basis for the experimental error.*

Therefore,

Total S. S. = Treatment S.S. + Block S.S. + Error S. S. Analysis of variance is given in table 118.

TABLE 118.

ANALYSIS OF VARIANCE.

Variance due to.	D.F.	S.S.	Mean S.S.	F. valve. From Expt.	From Tables.
Blocks ...	4	1877·1	469·3	4·46	2·87
Treatments ...	5	2869·9	573·9	5·46	2·71
Residual Error ...	20	2103·3	105·2		
Total ...	29	6850·3			

Treatment and Block : Significant.

In the experiment it is to be tested whether the variations due to blocks and treatments are significant, (*i.e.*) whether the differences between yields of different treatment or blocks have occurred due to inherent difference or due to chance causes. This is done by calculating *variance ratio* (F). For blocks ' F ' is given by the mean variance for blocks divided by mean variance for error, *i.e.*, 469·3 ÷ 105·2 = 4·46. Similarly, for treatment, F is given by mean variance for treatment divided by mean variance for error, *i.e.*, 573·9 ÷ 105·2 = 5·46.

From the table of F (*vide* Appendix . .) at 5% level for $n_1 = 6$ (degrees of freedom corresponding to the larger mean square), and $n_2 = 20$ (degrees of freedom corresponding to the smaller mean), F = 2·71.

Since the ' F ' value from the experiment is greater than the ' F ' value from the tables, the observed variations due to treatment are significant.

It is to be considered which of the varieties are superior in yield to the control or standard. For this purpose, *critical difference* (C.D.) is calculated from Fisher's formula.

C.D. = t × S.E. of difference between means.

$$= t \times \sqrt{\frac{2 \times 105{\cdot}2}{5}}$$

= 13·56.

For degrees of freedom 20, value of t at 5% level from tables (*vide* Appendix I), is 2·09. Therefore C. D. between any two varieties = 13·56. Difference between the mean yields of any two plots must be 13·56 or more to be significant. Any difference which is less than 13·56 is not significant and is likely to have occurred due to chance.

The results are summarised by writing down the varieties in descending order of their mean yields, and connecting by a bar placed above or below as shown hereunder.

D. A. B. E. C. standard.

The differences in yield between the cultures D, A and B are due to chance ; but these three are distinctly superior in yield to E, C and standard (*vide* section 16).

13. Latin Square.—This is an improved lay-out over randomised blocks. The arrangement of plot is done in a way to eliminate errors due to soil heterogeneity in two directions at right angles to each other. *As the term " latin square " indicates, there should be as many replications as treatments so that the lay-out forms a square but does not necessarily connote that individual plots should be squares.* This method is applicable only when the number of variants is limited from 4 to 9. If the treatments are larger in number, there is no gain in precision by reduction of error on account of the unwieldy size of the experimental block. *The main principle to be observed in this lay-out is that there should be as many replications as there are treatments, and though the treatments are randomised within each replication, no one treatment can occur more than once in any particular column or row.* For example, if there are four treatments ABCD, they are arranged in 16 plots laid out in a square fashion 4×4. The randomisation is restricted to the location of the treatments in the row and columns as will be seen from table 119.

The data from such an experiment are analysed in a fashion more or less similar to that of randomised blocks with the difference that the block effect is calculated both for the columns and rows. By so doing, the random error of the experiment is considerably reduced and therefore the precision of the experiment is greater than that of randomised block. But, if the treatments are few in number, say 2 or 3, there is a defect if this method is adopted. The number of degrees of freedom is low. Also if the treatments are large in number the precision is lost, on account of unwieldy size of the total area for the experiment.

Table 119 gives weight of seed cotton in respect of an experiment in which 4×4 is adopted.

TABLE 119.

	Columns.				Total for rows.
Rows ...	A 52	B 47	C 46	D 54	199
	B 41	A 39	D 43	C 43	166
	C 46	D 34	A 41	B 27	148
	D 35	C 44	B 16	A 38	133
Total for Columns.	174	164	146	162	646

The yield data may be re-arranged as shown in table 120.

TABLE 120.

Treatment.	Replications. I.	II.	III.	IV.	Total.
A ...	52	39	41	38	170
B ...	47	41	27	16	131
C ...	46	43	46	44	179
D ...	54	43	34	35	166
Total ...	199	166	148	133	646

$$\text{Correction factor } \frac{646^2}{16} = 26{,}082{\cdot}3.$$

The computation of S. S. for total, treatment, columns, rows and error is similar to that in randomised blocks and is shown below :

TABLE 121.

TABLE OF SQUARES.

	Squares of individual plot yields (from Table 120).				Total.	S.S. for Columns.	S.S. for rows.
	2,704	1,521	1,681	1,444	7,350	30,276	39,601
	2,209	1,681	729	256	4,875	26,896	27,556
	2,116	1,849	2,116	1,936	8,017	21,316	21,904
	2,916	1,849	1,156	1,225	7,146	26,244	17,689
Total ...	9,945	6,900	5,682	4,861	27,388	104,732	106,750

Analysis of variance is shown in table 122.

TABLE 122.

Variance due to.	D.F.	S.S.	Mean S.S.	F. value. From Expt.	From Tables
Rows .	3	606	202	4·6	
Columns .	3	101	34	0·8	
Treatment	3	333	111	2·5	4·76
Error .	6	266	44		
Total	15	1,306			

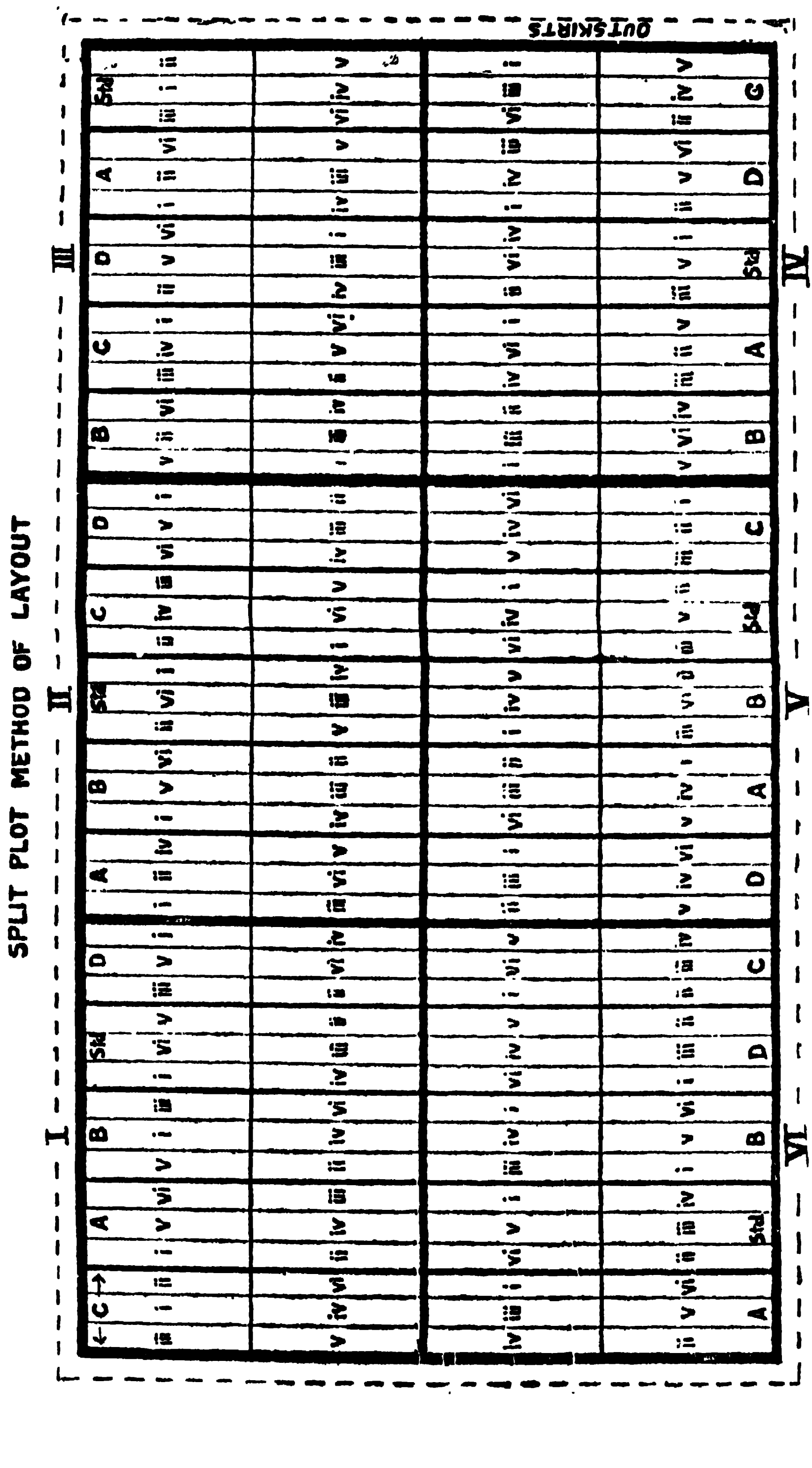


Fig. 159. Field Plan.

In this experiment, there is no difference in yield due to treatments, *i.e.*, the observed differences are *not significant.*

When the observed differences are significant, critical difference is calculated and the superiority of the treatments judged as described under randomised blocks.

14. Split plot design.—This lay-out is very useful for adoption in experiments wherein two factors differing much in their extent of variation are under study. These factors are grouped as *main* and *sub* treatments. For example, if it is desired to test a few varieties under differing sowing dates, the variation expected between varieties is likely to be less than what is expected due to the differences in sowing dates. Therefore, a greater precision is necessary in the factor with lower variation. The factor with bigger variation forms the main treatment in the lay-out and is bound to lose a certain amount of precision as compared to sub-treatments.

This method of lay-out has the advantage of furnishing the extent of interaction between the two sets of treatments—*viz.*, main and sub-treatments. Experiments involving different agronomic treatments very much differing in their *modus operandi*, e.g., irrigation combined with manures, it is helpful to separate such treatments as main and sub-treatments.

The treatments are arranged as follows :—

The land selected is divided into blocks representing replications. Then each block is sub-divided into as many equal parts as there are main treatments. Then each sub-plot is equally divided into as many plots of equal size as there are sub-treatments. The sub-treatments are randomised and fixed within each main treatment plot. In turn the main treatment plots are randomised within each block.

This lay-out is useful to plant breeders in the course of selection of improved strains. In the early stages of selection in different hybrid progenies, this lay-out is adopted to test the superiority of any of the families as well as selection within the families. For example, if there are four families of cultures in cotton designated A, B, C and D and if there are 6 selections within each one of these five families, split plot design may be adopted for further selection of improved types. These four families are progenies from different crosses and they have proved useful in row yield trial. Six single plants have been selected in each family. Further tests are intended to test the superiority between the families and between sibs within the families. In this lay-out all the cultures falling within a family (hybrid line) are grouped together and this test is designated as "*Compact family block*" (Hutchinson and Panse 1936).

Lay-out and analysis of data are illustrated below (*vide* fig. 159).

TABLE 123.

Family.	Sib within family.	Replications. I.	II.	III.	IV.	V.	VI.	Total for Sibs.	Total for family.
A	i	5	6	8	7	9	5	40	297
	ii	10	8	7	11	9	10	55	
	iii	7	8	6	9	6	7	43	
	iv	12	14	10	9	11	13	69	
	v	9	7	11	8	9	11	55	
	vi	8	5	7	6	4	5	35	
		51	48	49	50	48	51	...	297
B	i	6	5	4	5	6	7	33	
	ii	5	7	5	6	7	8	38	
	iii	8	7	6	5	8	7	41	
	iv	9	7	6	8	9	7	46	
	v	5	6	7	5	5	7	35	
	vi	7	8	10	9	8	7	49	
		40	40	38	38	43	43	...	242
C	i	12	14	16	14	15	13	84	
	ii	15	13	11	12	16	15	82	
	iii	16	12	11	9	10	13	71	
	iv	14	16	15	13	10	12	80	
	v	12	14	11	10	13	16	76	
	vi	15	11	10	9	13	12	70	
		84	80	74	67	77	81	...	463
D	i	7	6	5	4	5	5	32	
	ii	6	7	5	4	5	4	31	
	iii	8	7	5	6	6	5	37	
	iv	7	6	5	4	6	7	35	
	v	5	4	6	7	5	5	32	
	vi	8	7	6	6	4	6	37	
		41	37	32	31	31	32	...	204
Standard	i	8	7	6	6	7	8	42	
	ii	7	9	8	6	9	10	49	
	iii	8	6	7	9	7	8	45	
	iv	6	7	7	8	9	8	45	
	v	10	8	9	7	8	9	51	
	vi	8	7	8	9	9	10	51	
		47	44	45	45	49	53	...	283
		263	249	238	231	248	260	...	1,489

$$\text{Correction factor} = \frac{1489^2}{180}$$
$$= 12317{\cdot}3.$$

The yield data in table 123 may be re-arranged as shown in table 124 to bring out the yield of families in the six replications.

TABLE 124.

TOTALS FOR MAIN TREATMENTS.

Families.	Replications.						Total.	Mean.
	I.	II.	III.	IV.	V.	VI.		
A	51	48	49	50	48	51	297	8·25
B	40	40	38	38	43	43	242	6·72
C	84	80	74	67	77	81	463	12·86
D	41	37	32	31	31	32	204	5·67
Standard.	47	44	45	45	49	53	283	7·86
	263	249	238	231	248	260	1,489	

Total S. S. is derived by summating the squares of 180 individual readings (table 123) and applying the correction factor as shown in table 125.

TABLE 125.

TOTAL S.S.

Family.	Sibs within family.	Replications. I.	II.	III.	IV.	V.	VI.	Total for Sibs.	Total for family.
A	i	25	36	64	49	81	25	280	
	ii	100	64	49	121	81	100	515	
	iii	49	64	36	81	36	49	315	
	iv	144	196	100	81	121	169	811	
	v	81	49	121	64	81	121	517	
	vi	64	25	49	36	16	25	215	2,653
B	i	36	25	16	25	36	49	187	
	ii	25	49	25	36	49	64	248	
	iii	64	49	36	25	64	49	287	
	iv	81	49	36	64	81	49	360	
	v	25	36	49	25	25	49	209	
	vi	49	64	100	81	64	49	407	1,698
C	i	144	196	256	196	225	169	1,186	
	ii	225	169	121	144	256	225	1,140	
	iii	256	144	121	81	100	169	871	
	iv	196	256	225	169	100	144	1,090	
	v	144	196	121	100	169	256	986	
	vi	225	121	100	81	169	144	840	6,113
D	i	49	36	25	16	25	25	176	
	ii	36	49	25	16	25	16	167	
	iii	64	49	25	36	36	25	235	
	iv	49	36	25	16	36	49	211	
	v	25	16	36	49	25	25	176	
	vi	64	49	36	36	16	36	237	1,202
Standard ...	i	64	49	36	36	49	64	298	
	ii	49	81	64	36	81	100	411	
	iii	64	36	49	81	49	64	343	
	iv	36	49	49	64	81	64	343	
	v	100	64	81	49	64	81	439	
	vi	64	49	64	81	81	100	439	2,273
									13,939

Total S. S. $=13{,}939-12317\cdot3$

$=1621\cdot7$

Total yield from six replications for each family and sib is shown in table 126.

TABLE 126.

INTERACTION TABLE.

Family. \ Sibs.	i.	ii.	iii.	iv.	v.	vi.	Total.
A	40	55	43	69	55	35	297
B	33	38	41	46	35	49	242
C	84	82	71	80	76	70	463
D	32	31	37	35	32	37	204
Standard	42	49	45	45	51	51	283
Total ...	231	255	237	275	249	242	1,489

The variance due to block, main plot, family, sibs and interaction are calculated as shown below :

$$\text{Block S. S.} = \frac{263^2 + 249^2 \ldots\ldots\ldots 260^2}{30} - 12317{\cdot}3 \text{ (correction factor).}$$

(*vide* table 124).

$$= 25{\cdot}3$$

The total for each block consists of 5 families with 6 sibs in each family or 30 plots. Therefore the S. S. is divided by 30 to get mean square for block.

$$\text{Main plot S. S.} = \frac{51^2 + 48^2 \ldots\ldots 49^2 + 53^2}{6} - 12317{\cdot}3$$

(*vide* table 124).

$$= 1154{\cdot}9$$

Each main plot consists of 6 sibs and hence the total of squares from 30 main plots is divided by 6 and correction factor applied.

$$\text{Family S. S.} = \frac{297^2 + 242^2 \ldots\ldots + 283^2}{36} - 12{,}317{\cdot}3$$

(*vide* table 10).

$$= 1095{\cdot}1$$

Each family total consists of 6 sibs in 6 replications or 36 plots. Hence the total of squares is divided by 36 and correction factor applied.

$$\text{Sibs S. S.} = \frac{231^2 + 255^2 \ldots\ldots + 242^2}{30} - 12{,}317{\cdot}3$$

(*vide* table 126).

$$= 40{\cdot}9$$

$$\text{Interaction, Family} \times \text{Sib.} = \frac{40^2 + 55^2 \ldots\ldots + 51^2 + 51^2}{6} - 12{,}317{\cdot}3 - (1095{\cdot}1 + 40{\cdot}9)$$

$$= 167{\cdot}9$$

The analysis of variance is summarised in table 127.

TABLE 127.

ANALYSIS OF VARIANCE.

Variance due to.	D.F.	S.S.	Mean S.S.	F. From Expt.	F. From Tables.
Blocks	5	25·3	5·1	3·0	2·71
Between Families ...	4	1095·1	273·8	161·0	2·87
Error (*a*) ...	20	34·5	1·7		
Total main plots ...	29	1154·9			
Within families between sibs ...	5	40·9	8·2	2·9	2·29
Interaction (Family and Sib.) ...	20	167·9	8·4	4·0	1·65
Error (*b*)	125	258·0	2·1		
Total ...	179	1,621·7			

In applying F test for significance, *error* (a) *is taken for comparing the main treatments and error* (b) *is taken for comparing the sub-treatments* (*viz., sibs within the families*). In the above example, variations between families and between sibs are *significant.*

C. D. for main treatments $= t \times S.E.$

$$= 2{\cdot}09 \times \sqrt{\frac{2 \times 1{\cdot}7}{6}}$$

$= 1{\cdot}58$ per plot.

C. D. for sub-treatments $= t \times S.E.$

$$= 1{\cdot}98 \times \sqrt{\frac{2 \times 2{\cdot}1}{6}}$$

$= 1{\cdot}66$ per plot.

The following conclusion shows the relative merits between the families :

C. A. Standard B. D.

Family C is outstandingly superior to all other families.

Similarly, the superiority of sibs within the families is worked out.

15. Lattice Design.—This method of lay-out is advantageously adopted when a fairly large number of varieties has to be tested at the same time and the size of individual plots has necessarily to be kept big as in the case of yield trials under rainfed conditions in the cereals. Due to the large size of individual plots, block size is considerably increased and variation due to soil heterogeneity cannot be effectively controlled if the ordinary method of randomised block is adopted. Hence Yates has designed this particular lay-out where large number of varieties can be tested at the same time with a fairly high degree of experimental precision. Another advantage in this lay-out is that, if due to any unforeseen causes, a portion of the experimental crop is affected, still the results from the remaining blocks give ample scope for analysis and valid deduction of conclusions.

In a simple lattice design lay-out, the number of varieties to be tested must form a square, e.g. 3×3, 4×4, 5×5, etc. The lay-out and analysis are illustrated by taking a varietal trial in horsegram with 64 selections.

Method of lay-out.—The sixty-four varieties are serially numbered 1 to 64 and arranged in a square as follows : The number of varieties (r) is divided into blocks of 8 varieties (k) each.

Rows.

Columns.

1	2	3	4	5	6	7	8
9	10	11	12	13	14	15	16
17	18	19	20	21	22	23	24
25	26	27	28	29	30	31	32
33	34	35	36	37	38	39	40
41	42	43	44	45	46	47	48
49	50	51	52	53	54	55	56
57	58	59	60	61	62	63	64

Fig. 160.

There are 8 rows and 8 columns in the above square. The 64 varieties are divided into two groups designated X and Y. Each one of the 8 blocks in a replication of x group, is formed by the rows in the square (Fig. 160). The position of blocks and the position of varieties in the block are randomised. In the field plan shown in fig. 161 varieties 1 to 8 of x group fall in block 2 and the position of varieties in the 8 plots is further randomised and they are arranged in the order 5, 1, 2, 8, 7, 4, 3, 6, in replication I.

Group y is constituted by taking the varieties in the column of the square. Thus, varieties 1, 9, 17, 25, 33, 41, 49 and 57 constitute a block. As in the case of x group, the position of the blocks and the varieties are randomised. In the field plan shown in fig. 161 the abovementioned group falls into the fourth block and the varieties are arranged in the order 9, 49, 33, 1, 57, 25, 17, 41 in replication II. Each group of x and y is replicated twice. *There are four replications and all the 64 varieties occur once in each replication. The blocks are incomplete in that all the 64 varieties do not occur in each block.*

X	Y
I	II
III	IV

Fig. 161. FIELD PLAN FOR LATTICE DESIGN WITH 64 VARIETIES.
(VARIETY NUMBER IN BOLD TYPES.)
(YIELD IN TOLAS PER PLOT.)

TABLE 128.
GROUP X.
Replication I.

BLOCK.									BLOCK Total.
1	**55**	**51**	**56**	**50**	**49**	**54**	**52**	**53**	
	25·3	24·4	23·1	27·0	9·8	17·0	17·3	31·9	175·8
2	**5**	**1**	**2**	**8**	**7**	**4**	**3**	**6**	
	30·6	25·5	12·0	19·8	14·1	30·0	31·4	27·0	190·4
3	**23**	**20**	**17**	**24**	**21**	**19**	**22**	**18**	
	29·1	27·8	27·5	24·3	13·5	10·5	17·3	23·5	173·5
4	**62**	**64**	**57**	**59**	**63**	**58**	**61**	**60**	
	21·3	25·9	16·5	20·0	12·4	13·5	20·0	10·9	140·8
5	**44**	**48**	**47**	**41**	**45**	**42**	**46**	**43**	
	13·1	18·4	18·0	18·9	10·8	3·8	12 3	30·8	126·1
6	**38**	**33**	**39**	**36**	**37**	**34**	**35**	**40**	
	25·9	9·0	10·6	23·1	7·3	26·8	14·1	22·9	139·7
7	**28**	**31**	**25**	**29**	**30**	**27**	**32**	**26**	
	9·6	17·1	27·3	23·1	12·4	27·6	17·3	25·5	159·9
8	**12**	**9**	**14**	**16**	**11**	**15**	**10**	**13**	
	21·5	18·9	10·1	10·8	9·1	15·5	26·4	35·3	147·6
									1253·8

TABLE 129.
GROUP Y.
Replication II.

BLOCK.									BLOCK Total.
9	**20**	**60**	**44**	**28**	**52**	**12**	**4**	**36**	
	26·5	16·5	19·6	20·5	16·6	33·0	30 0	18·4	181·1
10	**48**	**24**	**16**	**40**	**64**	**56**	**32**	**8**	
	17·0	24·8	21·9	34·9	28·9	37·8	22·5	15·9	203·7
11	**29**	**53**	**21**	**13**	**45**	**5**	**37**	**61**	
	23·5	15·4	15·8	30·8	18·9	23·6	18·8	27·1	173·9
12	**9**	**49**	**33**	**1**	**57**	**25**	**17**	**41**	
	14·9	12·1	12·1	23·3	26·0	19·1	19·8	23·6	150·9
13	**59**	**19**	**11**	**51**	**35**	**3**	**43**	**27**	
	9·5	13·3	9·5	18·8	8·9	19·8	32·3	20·6	132·7
14	**15**	**39**	**55**	**63**	**7**	**47**	**23**	**31**	
	14·4	18·4	16·8	8·1	12·1	23·8	25·4	27·5	146·5
15	**26**	**18**	**42**	**10**	**34**	**50**	**2**	**58**	
	15·3	22·1	5·5	8·3	21·4	19·8	7·6	3·9	103·9
16	**62**	**6**	**14**	**54**	**46**	**30**	**22**	**38**	
	17·4	23·9	10·1	16·0	7·3	7·8	14·5	16·3	113·3
									1206·6

Fig. 161. FIELD PLAN FOR LATTICE DESIGN WITH 64 VARIETIES—(*contd.*)
(VARIETY NUMBER IN BOLD TYPES.)

(YIELD IN TOLAS PER PLOT.)

TABLE 130.
GROUP X.
Replication III.

BLOCK.									BLOCK Total.
17	**40**	**37**	**39**	**35**	**32**	**38**	**36**	**34**	
	19·5	15·5	24·1	8·9	11·3	15·0	28·5	22·3	145·1
18	**60**	**64**	**57**	**59**	**63**	**61**	**58**	**63**	
	18·4	18·4	20·4	22·1	28·3	17·9	25·3	15·6	166·4
19	**50**	**53**	**56**	**55**	**51**	**49**	**52**	**54**	
	21·8	18·6	20·9	15·6	22·0	15·8	28·5	19·6	162·8
20	**44**	**46**	**48**	**42**	**41**	**45**	**43**	**47**	
	14·5	9·5	7·9	22·9	13·0	19·5	21·8	27·5	136·6
21	**4**	**7**	**8**	**2**	**1**	**3**	**6**	**5**	
	22·1	20·0	11·8	16·3	18·0	17·5	20·8	20·6	147·1
22	**9**	**13**	**16**	**15**	**12**	**11**	**14**	**10**	
	10·5	23·3	14·4	9·0	17·1	8·5	11·6	13·0	107·4
23	**28**	**32**	**30**	**25**	**29**	**26**	**31**	**27**	
	13·0	12·3	20·5	26·1	23·0	21·8	23·8	19·0	159·5
24	**21**	**23**	**17**	**20**	**22**	**19**	**24**	**18**	
	8·8	20·8	14·4	22·6	15·0	11·0	12·0	18·0	122·7
									1147·6

TABLE 131.
GROUP Y.
Replication IV.

BLOCK.									BLOCK Total.
25	**16**	**40**	**32**	**56**	**24**	**64**	**8**	**48**	
	10·8	15·8	17·5	16·1	12·1	26·1	7·8	17·4	123·6
26	**58**	**34**	**10**	**42**	**2**	**26**	**18**	**50**	
	11·3	22·3	15·0	11·6	17·5	10·8	16·0	14·1	118·6
27	**54**	**38**	**46**	**62**	**14**	**30**	**6**	**22**	
	14·6	27·9	20·0	13·8	15·0	8·6	20·3	14·0	134·2
28	**49**	**17**	**41**	**25**	**57**	**9**	**1**	**33**	
	7·5	10·8	15·6	9·9	13·3	16·5	23·4	11·4	108·4
29	**3**	**51**	**27**	**19**	**43**	**11**	**59**	**35**	
	8·8	21·1	21·9	22·9	29·5	10·0	9·0	14·1	137·3
30	**29**	**37**	**45**	**13**	**53**	**21**	**61**	**5**	
	16·5	7·3	16·0	12·3	11·3	8·8	5·9	22·0	100·1
31	**4**	**12**	**20**	**28**	**36**	**44**	**52**	**60**	
	25·0	21·5	23·1	7·9	15·9	16·1	11·8	11·0	132·3
32	**33**	**55**	**47**	**39**	**31**	**23**	**15**	**7**	
	8·5	7·6	12·8	18·0	15·0	17·8	5·3	7·5	92·5
									947.0

TABLE 132.

GROUP X.

Combination of Replications I & III.

									Row Total.
	1 43·5	2 28·3	3 48·9	4 52·1	5 51·2	6 47·8	7 34·1	8 31·6	337·5
	9 29·4	10 39·4	11 17·6	12 38·6	13 58·6	14 21·7	15 24·5	16 25·2	255·0
	17 41·9	18 41·5	19 21·6	20 50·4	21 22·3	22 22·3	23 49·9	24 36·3	286·2
	25 43·4	26 47·3	27 46·6	28 22·6	29 46·1	30 33·3	31 40·9	32 29·6	309·8
	33 20·3	34 49·1	35 31·6	36 51·6	37 22·8	38 40·9	39 34·7	40 42·4	293·4
	41 31·9	42 26·7	43 52·6	44 27·6	45 30·3	46 21·8	47 45·5	48 26·3	262·7
	49 25·6	50 48·8	51 46·4	52 45·8	53 50·5	54 36·6	55 40·9	56 44·0	338·6
	57 36·9	58 39·1	59 42·1	60 29·3	61 37·9	62 48·6	63 28·0	64 44·3	306·2
Column Total.	272·9	320·2	307·4	318·0	319·7	273·0	298·5	279·7	2389·4

TABLE 133.

Combination of Replications II & IV.

									Row Total.
	1	9	17	25	33	41	49	57	
	50·7	31·4	30·6	29·0	24·3	39·2	19·6	39·3	264·1
	2	10	18	26	34	42	50	58	
	25·1	23·3	38·1	26·1	43·7	17·1	33·9	15·2	222·5
	3	11	19	27	35	43	51	59	
	28·6	19·5	36·2	42·5	25·4	61·8	39·9	18·5	272·4
	4	12	20	28	36	44	52	60	
	55·0	54·5	49·6	28·4	34·3	35·7	28·2	27·5	313·2
	5	13	21	29	37	45	53	61	
	45·6	43·1	23·8	40·0	26·1	34·9	26·7	26·8	267·0
	6	14	22	30	38	46	54	62	
	44·2	26·1	28·5	16·4	44·2	27·3	30·6	31·2	248·4
	7	15	23	31	39	47	55	63	
	19·6	19·7	43·2	42·5	36·4	36·6	24·4	16·6	239·0
	8	16	24	32	40	48	56	64	
	23·7	32·7	36·9	40·0	50·7	34·4	53·9	55·0	327·3
Column Total.	292·5	250·3	286·9	264·9	285·1	287·0	257·2	230·1	2154·0

Computation.—The total yields of varieties are re-arranged as shown in table 134.

TABLE 134.

TOTAL YIELD OF VARIETIES.

									Row Total.
	1	2	3	4	5	6	7	8	
	94·2	53·4	77·5	107·1	96·8	92·0	53·7	55·3	630·0
	9	10	11	12	13	14	15	16	
	60·8	62·7	37·1	93·1	101·7	47·8	44·2	57·9	505·3
	17	18	19	20	21	22	23	24	
	72·5	79·6	57·8	100·0	46·1	50·8	93·1	73·2	573·1
	25	26	27	28	29	30	31	32	
	72·4	73·4	89·1	51·0	86·1	49·7	83·4	69·6	574·7
	33	34	35	36	37	38	39	40	
	44·6	92·8	57·0	85·9	48·9	85·1	71·1	93·1	578·5
	41	42	43	44	45	46	47	48	
	71·1	43·8	114·4	63·3	65·2	49·1	82·1	60·7	549·7
	49	50	51	52	53	54	55	56	
	45·2	82·7	86·3	74·0	77·2	67·2	65·3	97·9	595·8
	57	58	59	60	61	62	63	64	
	76·2	54·3	60·6	56·8	64·7	79·8	44·6	99·3	536·3
Column Total ...	537·0	542·7	579·8	631·2	586·7	521·5	537·5	607·0	4543·4

Total S. S. is calculated by squaring the 256 plot yields in tables 128, 129, 130 and 131 and applying the correction factor :

$$(25{\cdot}3^2 \;\ldots\; 26{\cdot}3^2 + \;\ldots\; 19{\cdot}5^2 \ldots\; 10{\cdot}8^2 + \ldots) - \frac{4543{\cdot}4^2}{256}$$

$$= 92696{\cdot}3 - 80634{\cdot}7$$
$$= 12061{\cdot}6$$

S. S. for replications =

$$\frac{1253{\cdot}8^2 + 1206{\cdot}0^2 + 1147{\cdot}6^2 + 947{\cdot}0^2}{64} - 80634{\cdot}7$$

$$= 244{\cdot}$$

S. S. for varieties is calculated from varietal totals given in table 134.

$$\frac{94{\cdot}2^2 + \ldots\ldots\ldots 99{\cdot}3^2}{4} - 80634{\cdot}7$$

$$= 6041{\cdot}1$$

S. S. for blocks has two components 'a' and 'b'. Component 'a' is calculated from the differences between blocks having the same set of varieties. This is shown in table 135.

TABLE 135.

Set X.				Set Y.			
Repli-cation. I	Repli-cation. III	Differ-ence.	Square of difference.	Repli-cation. II	Repli-cation. IV	Differ-ence.	Square of difference.
190·4	147·1	43·3	1,874·89	150·9	108·4	42·2	1,806·25
147·6	107·4	40·2	1,616·04	103·9	118·6	—14·7	216·09
173·4	122·7	50·7	2,570·49	132·7	137·3	—4·6	21·16
159·9	159·5	0·4	0·16	181·1	132·3	48·8	2,381·44
139·7	145·1	—5·4	29·16	173·9	100·1	73·8	5,446·44
126·1	136·6	—10·5	110·25	113·3	134·2	—20·9	436·81
175·8	162·8	13·0	169·00	146·5	92·5	54·0	2,516·00
140·8	166·4	—25·6	655·36	203·7	123·6	80·1	6,416·01
1,253·7	1,147·6	106·1	7,025·35	1,206·0	947·0	259·0	1,9640·2

S. S. for blocks. Component 'a'

$$\frac{7025{\cdot}35}{16} \quad \frac{19{,}640{\cdot}2}{16} \quad \frac{(106{\cdot}1^2+259{\cdot}0^2)}{128}$$

$= 1054{\cdot}6$

Component '*b*' is calculated from difference giving estimates of block yields freed from varietal differences. These differences are termed rKc_x and rKc_y where y represents the number of replications, K is number of plots per block and C_x and C_y are respectively mean corrections from x and y groups.

TABLE 136.

COMPONENT '*b*'.

rKCx.				rKCy			
630·0	—2 (337·5)	—45·0	2,025·0	537·0	—2 (264·1)	8·8	77·44
505·3	—2 (225·0)	—4·7	22·09	542·7	—2 (222·5)	97·7	9,545·29
573·1	—2 (286·2)	0·7	0·49	578·8	—2 (272·4)	35·0	1,225·00
574·7	—2 (309·8)	44·9	2,016·01	631·2	—2 (313·2)	4·8	23·04
578·5	—2 (293·4)	—8·3	68·89	586·7	—2 (267·0)	52·7	2,777·29
549·7	—2 (262·7)	—24·3	590·49	521·5	—2 (248·5)	24·5	600·25
598·8	—2 (338·6)	—81·4	6,625·96	537·5	—2 (239·0)	59·5	3,540·25
526·3	—2 (306·2)	—76·1	5,791·21	607·0	—2 (327·3)	—47·6	2,265·76
		—235·4	17,140·14			235·4	20,054·32

$$\text{Component } `b' = \frac{17140{\cdot}14+20054{\cdot}32}{32}$$

$$\frac{(-235{\cdot}4)^2+(235{\cdot}4)^2}{256}$$

$$=729{\cdot}4$$

Analysis of variance is shown in table 137.

TABLE 137.

Variance due to.	D.F.	S.S.	Mean.
Replications	3	1,244·1	414·7
Component (*a*)	14	1,054·6	75·3
Component (*b*)	14	729·4	52·1
Blocks	28	1,784·0	63·7
Varieties	63	6,041·1	95·9
Error	161	2,992·4	18·6
Total	255	12,061·6	47·3

Significance may be judged by applying the F test as in the case of randomised block (Table 138).

TABLE 138.

Variance due to.	D.F.	S.S.	Mean S.S.	F. value. From Expt.	F. value. From tables.
Replications ...	3	1,244·1	414·7	16·4	2·65
Varieties ...	63	6,041·1	95·9	3·8	1·39
Error ...	189	4,776·4	25·3	...	...
Total ...	255	12,061·6	47·3	...	...

The differences between the varieties are *significant*.

The above method of testing significance is not precise but is generally adequate for the purpose.

The average yields of varieties are calculated from table 134. These averages are to be corrected for differences between blocks. The corrections are applied to get the adjusted yields. If the mean square for blocks (B) is less than or equal to the mean square for error (E) in table 137, the average yields may be taken as such without correction. If B is greater than E the correction is carried out as follows :

$$\text{Weighing factor} = \frac{W-W^1}{W+W^1}$$

$$W=\frac{1}{E}=\frac{1}{18{\cdot}6}=0{\cdot}054.$$

$$W^1=\frac{3}{4B-E}=\frac{}{4\times63{\cdot}7-18{\cdot}6}=0{\cdot}013$$

∴ Weighing factor

$$\frac{0{\cdot}054-0{\cdot}013}{0{\cdot}054+0{\cdot}013}=0{\cdot}612.$$

$$Cx^1=\frac{1}{r\times k}\,\frac{(W-W^1)}{W+W^1}\,rKC_x$$

$$=\frac{1}{4\times8}\,(0{\cdot}612)\,rKC_x$$

$$=0{\cdot}019\,rKC$$

$$Cy^1=\frac{1}{r\times k}\left(\frac{W-W^1}{W+W^1}\right)rKC_y$$

$$=\frac{1}{4\times8}\,(0{\cdot}612)\,rKC_y$$

$$=0{\cdot}019\,rKC_y$$

(r=replications ; K=number of varieties in a block).
Values of rKC_x and rKC_y are taken from Table 136.

Average yield of the varieties is obtained by dividing the total yields (in table 134) by 4 (*vide* table 139).

TABLE 139.

	1	2	3	4	5	6	7	8	
	23·6	13·6	19·4	26·8	24·2	23·0	13·4	13·8	—0·64
	9	10	11	12	13	14	15	16	
	15·2	15·7	9·3	23·3	25·4	12·0	11·1	14·5	—0·67
	17	18	19	20	21	22	23	24	
	18·1	19·9	14·5	25·0	11·5	12·7	23·3	18·3	0·10
	25	26	27	28	29	30	31	32	
	18·1	18·4	22·3	12·8	21·5	12·3	20·9	17·4	—0·64
	33	34	35	36	37	38	39	40	
	11·2	23·2	14·3	21·5	12·2	21·3	17·8	23·3	—0·12
	41	42	43	44	45	46	47	48	
	17·8	11·4	28·6	15·8	16·3	12·3	20·5	15·2	0·35
	49	50	51	52	53	54	55	56	
	11·3	20·7	21·6	18·5	19·3	16·8	16·3	24·5	—1·16
	57	58	59	60	61	62	63	64	
	19·1	13·6	15·2	14·2	16·2	20·0	11·2	24·8	—1·08
ry^1	0·12	1·42	0·50	0·07	0·75	0·35	0·84	—0·68	

The adjusted yield for each variety is calculated by adding rx^1 and ry^1 in the respective rows and columns. For example, the adjusted yield for variety 1=23·6—0·64+0·12=23·08. The adjusted yields are shown in Table 140.

TABLE 140.

1 23·08	2 12·82	3 19·26	4 26·23	5 24·31	6 22·71	7 13·6	8 12·48
9 14·65	10 16·45	11 9·13	12 22·70	13 25·48	14 11·68	15 11·27	16 13·15
17 18·32	18 21·42	19 15·10	20 25·17	21 12·35	22 13·15	23 24·24	24 17·72
25 17·58	26 19·18	27 22·16	28 12·23	29 21·61	30 12·01	31 21·10	32 16·08
33 11·20	34 24·5	35 14·68	36 21·45	37 12·83	38 21·53	39 18·52	40 22·50
41 18·27	42 12·17	43 29·45	44 16·22	45 17·40	46 13·0	47 21·69	48 14·87
49 10·27	50 20·96	51 20·94	52 17·41	53 18·89	54 15·99	55 15·98	56 22·66
57 18·14	58 13·94	59 14·62	60 13·19	61 15·87	62 19·27	63 10·96	64 23·04

The standard error of the difference between the means of two varieties occurring in the same block.

$$= \sqrt{2 \times \frac{\text{mean S. S. for error}}{\text{r. k.}}\left[\frac{2\,W}{W+W^1}\times(k-1)\right]}$$

The standard error of the difference between the means of two varieties that do not occur in the same block.

$$= \sqrt{2 \times \frac{\text{mean S. S. for error}}{\text{r. k.}}\left[\frac{4\,W}{W+W^1}+(k-2)\right]}$$

Lattice experiments may be analysed as in the case of randomised blocks, but then error is large and precision is less.

16. Co-variance.—Yields from different plots in an experiment may sometimes be correlated to any other important attribute affecting yield, *e.g.*, when the number of plants in different plots varies significantly, the yield data are not strictly comparable. Yields of different varieties on the basis of equal number of plants per plot are then to be estimated. This is done by calculating the sum of squares for the two attributes yield (y) and stand (x) and sums of products of yield and stand (xy) and analysing the variances. This method of analysis is termed *analysis of co-variance*.

The method of analysis of co-variance is illustrated by taking the data furnished under randomised blocks.

Table 141 shows the variation in the number of plants in the different plots (*i.e.*, Stand x).

TABLE 141.

(Number of plants per plot.)

Culture.	Replication. I.	II.	III.	IV.	V.	Total.	Mean.
A. ...	86	86	88	91	77	428	85·6
B. ...	93	85	84	93	86	441	88·2
C. ...	86	78	71	74	74	383	76·6
D. ...	86	83	83	83	81	416	83·2
E. ...	83	71	81	83	70	388	77·6
Std. ...	82	90	73	84	73	402	80·4
Total	516	493	480	508	461	2,458	

Grand mean $=81{\cdot}9$

Correction factor $=\dfrac{2458^2}{30}$

$=201392{\cdot}1$

S. S. Total for stand is calculated as shown in table 142 below :—

TABLE 142.

Culture.	Replication.					Total.
		II.	III.	IV.	V.	
A.	7,396	7,396	7,744	8,281	5,929	36,746
B.	8,649	7,225	7,056	8,649	7,396	38,975
C.	7,396	6,084	5,041	5,476	5,476	29,473
D.	7,396	6,889	6,889	6,889	6,561	34,624
E.	6,889	5,041	6,561	6,889	4,900	30,280
Std.	6,724	8,100	5,329	7,056	5,329	32,538
Total	44,450	40,735	38,620	43,240	35,591	2,02,636

Total S. S.=202636—201392·1=1243·9

S. S. for Treatments.	S. S. for Blocks.
183184	266256
194481	243049
146689	230400
173056	258064
150544	212521
161604	
	12,10,290
10,09,558	
1009558 -201392·	$\frac{1210290}{6}$ 201392·1
=519·5	=322·9

Analysis of variance for stand is shown in the following table 143.

TABLE 143.

Variation due to.	D.F.	S.S.	Mean S.S.	F. value. From Expt.	F. value. From tables.
Blocks	4	322·9	80·7	4·01	2·87
Treatments ...	5	519·5	103·9	5·17	2·71
Residual error ...	29	401·5	20·1	...	...
Total ...	29	1,243·9	...	...	...

Variations in stand due to blocks and treatments are *both significant.*

The product (xy) is then calculated by taking the yield (from table 116) and multiplying the same by the corresponding stand (from table 141). The calculations are shown in the following table :—

TABLE 144.

PRODUCT.

Culture.	Replications.					
		II.	III.	IV.	V.	
A.	7,138	6,192	8,536	6,916	5,236	34,018
B.	8,835	5,865	7,896	6,138	5,848	34,582
C.	4,816	4,836	4,970	4,588	4,218	23,428
D.	5,676	6,806	9,960	5,727	6,399	34,568
E.	6,059	3,692	6,237	5,063	3,780	24,831
Std.	4,756	5,850	4,015	5,208	3,869	23,698
	37,280	33,241	41,614	33,640	29,350	1,75,125

ction factor $= \dfrac{2458 \times 2121}{30}$

$= 173780{\cdot}6$

Total S.S. $= 175125 - 173780{\cdot}6$

$= 1344{\cdot}4$

S. S. for Treatment.		S. S. for Blocks.	
$428 \times 396 =$	169488	$516 \times 431 =$	222396
$441 \times 392 =$	172872	$493 \times 402 =$	198186
$383 \times 307 =$	117581	$480 \times 513 =$	246240
$416 \times 416 =$	173056	$508 \times 396 =$	201168
$388 \times 317 =$	122996	$461 \times 379 =$	174719
$402 \times 293 =$	117786		
			10,42,709
	8,73,779		

S. S. for Blocks $\dfrac{1042709}{6} - 173780{\cdot}6$

$= 4{\cdot}2$

S. S. for treatments $\dfrac{873779}{5} - 173780{\cdot}6$

$= 975{\cdot}2$

Analysis of variance for the product xy is shown in table 145.

TABLE 145.

Due to.	D.F.	S.S.
Blocks	4	4·2
Treatments	5	975·2
Residual Error	20	365·0
Total ...	29	1,344·4

Co-variance is calculated from the formula.

$$y^2+b^2x^2-2bxy$$

Where

y^2 stands for S. S. for yield.

x^2 stands for S. S. for stand.

xy stands for S. S. for product of yield and stand.

b is a regression factor derived from

$$\frac{\text{S. S. for residual error of xy}}{\text{S. S. for residual error of } x^2}$$

$$=\frac{365{\cdot}0}{401{\cdot}5}$$

$$=0{\cdot}91$$

Analysis of co-variance is shown in table 146 below :

TABLE 146.

Variance due to.	D.F.	y^2	x^2	xy.	$y^2+b^2x^2$ -2 bxy.	Means.	F. value. From Expt.	F. value. From Table.
Blocks ...	4	1,877·1	322·9	4·2	2,137·5	534·4	5·73	2·87
Treatments ...	5	2,869·9	519·5	975·2	1,526·2	305·2	3·27	2·71
Residual error.	19	2,103·3	401·5	365·0	1,772·2	93·3	...	...

Since F value from the experiment is greater than that from the tables, the variations due to treatments are *significant*.

The observed yields from the six cultures are now adjusted using the co-efficient ' b ' as shown in table 147 below :

TABLE 147.

Culture.	Mean yield y.	b.	Deviation of mean stand from grand mean stand 'd'.	bd.	y—bd. (adjusted yield).
A.	79·2	0·91	3·7	3·37	75·8
B.	78·4	...	6·3	5·73	72·7
C.	61·4	...	—5·3	—4·82	66·2
D.	83·2	...	1·3	1·18	82·0
E.	63·4	...	—4·3	—3·91	67·3
Std.	58·6	...	—1·5	—1·37	60·0

Final conclusions regarding the superiority of the cultures are tested by the application of critical difference as the minimum difference required for significance.

$$\text{C. D.} = \sqrt{\frac{2 \times 93 \cdot 3}{5}} \times t$$

$$= 12 \cdot 75$$

Conclusion :

$\overline{D}$, $\overline{A, B}$, *E*, *C Std.*

Chapter 26

HUMAN GENETICS

INTRODUCTION—COLOUR OF SKIN—SKIN TEXTURE—EYE—TASTE—BLOOD GROUPS—MN SERIES—RHESUS BLOOD GROUP—PRACTICAL APPLICATIONS

Introduction.—Mendel's laws of heredity were first discovered in plants and later confirmed in animals. Human beings are subject to the same fundamental laws of heredity as are other living organisms, plants or animals. For many reasons, study of inheritance of characters in man is more complicated than is the case with plants or other animals. Due to social reasons, strict pedigree culture methods are not applicable. Environment as a factor cannot be eliminated. Some characters are not completely understood and cannot be strictly defined and as such are difficult for genetic study. For example, " insanity" may involve twenty or more conditions of the human mind. Similarly, other psychological traits, including intelligence, are difficult to define or measure and as such are not easy of genetic analysis. The expression of characters or *penetrance* is low in human beings in respect of many characters. Human beings are capable to a large extent of controlling their own environment. For example, hemophilia (Bleeder's disease) may be suppressed from normal expression by blood transfusion. Similar is the case with susceptibility to diphtheria. The expression of the character depends upon infection being effectively carried to the individual. Artificial immunity may be induced in the susceptible individual by toxin-anti toxin treatments. Though the individual may have inherited susceptibility to the disease and may transmit it to the next generation too, the expression of the character depends on infection and artificial immunity may be induced by the modern medical treatments.

Colour of Skin.—The recessive gene for albino prevents development of pigment in eyes, skin and hair. Skin of black and yellow races seem to be governed by multiple genes. Negroes seem to differ from the whites by two pairs of genes. Mulattoes of Aa BB, AABb combinations are dark, those with Aa Bb, AA bb, aa BB are intermediate and those with Aabb, aabB are between intermediate and white. Differences between yellow and white races also are governed by several pairs. The genes for skin colour are also influenced by modifying genes.

Skin texture.—*Ichthyosis vulgaris* is an abnormality of the skin in which the skin is covered with small horny flakes or scales. This is due to dominant gene.

Some individuals cannot perspire. In hot weather, they cannot perspire to prevent the rise of body temperature. These individuals do not possess sweat glands and this is an inherited trait. Such persons cannot shed tears. This condition is governed by a recessive gene.

Eye.—The exact number of genes governing the colour of eye is not easy to determine. One pair of alleles seem to produce ' brown ' or ' blue ' but the brown colour is affected by other genes too. Congenital displacement of lens (*Ectopis lentis*) is caused by a dominant gene. Congenital cataract is caused by a dominant gene with incomplete penetrance.

Taste.—Ability to taste is a physiological trait. Phenylthiocarbamide tastes bitter for seven out of ten persons and is tasteless for three out of ten. Ability to taste is governed by a dominant gene while the double recessive cannot taste.

Blood groups.—The blood groups in human population are governed by multiple allelomorphs. There are two agglutinogens (A, B) in human beings. Any person may possess both, either or neither. Persons with agglutinogen A belong to ' A group ', with agglutinogen B to ' B group ' and those with neither belong to ' O group.' According to Landsteiner's rule, when a human adult lacks an *antigen*, he always possesses the corresponding *antibody*. Nobody lacks both the antigen and the antibody. Some individuals have agglutinin (antibody) for A, some for B and others have neither. If blood from group A person is injected into persons of groups A or AB, no harmful consequences arise, because the agglutinin or antibody is absent. Landsteiner (1900) working in Vienna discovered that if red blood cells of one person were mixed with blood serum of another, agglutination sometimes occurred. This did not happen in every case. Later investigations revealed that there were two antigens in human red cells and two corresponding antibodies in the serums. The genetic constitution of the four groups is represented in the following table :--

		Strandskov's gene symbols.
Group A ...	AO or AA	... I^Ai or I^AI^A
Group B ...	BO or BB	... I^Bi or I^BI^B.
Group AB ...	AB ...	... I^AI^B.
Group O ...	OO ...	... ii.

The blood group reactions are presented in the following table :—

Blood group.	Genotype. Bernsteins.	Genotype. Strandskov's.	Agglutinogens present.	Agglutinins present.	Groups whose serum will agglutinate cells of the group.	Groups whose cells will be agglutinated by serum of the group.
O	OO	ii	None	α, β	None	AB, A, B
A	AA, OA	I^AI^A, I^Ai	A	β	O, B	B, AB
B	BB, BO	I^BI^B, I^Bi	B	α	O, A	A, AB
AB	AB	I^AI^B	A, B	None	O, A, B	None

MN Series.—Independent of the AB group mentioned above, there are two other agglutinogens in human blood. All people may be classed as M, N or MN. Human beings rarely carry the agglutinins for these antigens. By injecting the blood into rabbits, antibodies are produced and the sera from such rabbits are again used to test the human blood. The MN group is inherited and three alleles are involved. M type is homozygous for M, N type for N and MN type is MN. The fact that an individual of M type cannot produce a child of N group is utilised in testing parentage of child in cases of doubt.

Rhesus blood groups.—If blood of rhesus monkey is injected into rabbits immune serum is produced in the blood of rabbits. If this serum is mixed with human blood, agglutination results in some cases. This agglutinogen is designated Rh, and is governed by a dominant gene R. In the case of a child born to Rh positive and Rh negative homozygous parents, the child will be of the genetic constitution Rr and Rh positive in reaction. The agglutinogen of foetus may pass through placenta to mother and the antibody may again diffuse back to the foetus and agglutinate its blood. This will result in still-born child, or the foetus may develop abnormalities including feeble mind. Sometimes, more than one pregnancy may be needed to develop the sensitisation.

Practical Application.—A number of heritable characteristics in man have been investigated and a few examples are listed below :—

Recessive genes.	*Dominant genes.*
1. Hemophilia (Sex linked).	1. Diabetes.
2. Albinism.	2. Auditory nerve atropy.
3. Blue or Grey eyes.	3. Congenital cataract.
4. Deaf Mutism.	4. Supernumerary teeth.
5. Red-green colour blindness.	5. Woolly hair.
6. Hare lip.	6. Pie balding.
	7. Dwarfism.

The basic laws of heredity are applicable to human beings. Most persons carry the recessive and harmful genes in heterozygous condition. When mating takes place with related persons, such as the first cousins, the defects or the diseases are expressed in the progenies. Normally, the chances of marriage between persons carrying harmful genes in heterozygous state are small, but if marriages between first cousins or closely related families are to be encouraged, the chances for hereditary defects appearing in homozygous form in the progenies are great. So long as desirable traits appear in homozygous form, it does not cause worry to the society. When undesirable traits like feeble mindedness, epilepsy, defective limbs, susceptibility to diseases etc.

appear, there is greater chance for quicker degeneration of the society. Study of the family history is not only important in deciding marriages, but also in the quick diagnosis of diseases. The application of genetics is useful in the investigation of disputed paternity and identification of individuals. In blood transfusions, blood tests for the genetic group are essential, as otherwise, the use of wrong blood will prove fatal.

The study of Eugenics is helpful in improving society. By study of family traits, marriage between persons that are likely to beget defective progenies due to genetic causes may be avoided. In extreme cases, sterilisation laws are promulgated to prevent undue and rapid multiplication of the defectives in society.

APPENDIX I.

DISTRIBUTION OF *t*.

Probability.

n	·9	·8	·7	·6	·5	·4	·3	·2	·1	·05	·02	·01	·001
1	·158	·325	·510	·727	1·000	1·376	1·963	3·078	6·314	12·706	31·821	63·657	636·619
2	·142	·289	·445	·617	·816	1·061	1·386	1·886	2·920	4·303	6·965	9·925	31·598
3	·137	·277	·424	·584	·765	·978	1·250	1·638	2·353	3·182	4·541	5·841	12·941
4	·134	·271	·414	·569	·741	·941	1·190	1·533	2·132	2·776	3·747	4·604	8·610
5	·132	·267	·408	·559	·727	·920	1·156	1·476	2·015	2·571	3·365	4·032	6·859
6	·131	·265	·404	·553	·718	·906	1·134	1·440	1.943	2·447	3·143	3·707	5·959
7	·130	·263	·402	·549	·711	·896	1·119	1·415	1·895	2·365	2·998	3·499	5·405
8	·130	·262	·399	·546	·706	·889	1·108	1·397	1·860	2·306	2·896	3·355	5·041
9	·129	·261	·398	·543	·703	·883	1·100	1·383	1·833	2·262	2·821	3·250	4·781
10	·129	·260	·397	·542	·700	·879	1·093	1·372	1·812	2·228	2·764	3·169	4·587
11	·129	·260	·396	·540	·697	·876	1·088	1·363	1·796	2·201	2·718	3·106	4·437
12	·128	·259	·395	·539	·695	·873	1·083	1·356	1·782	2·179	2·681	3·055	4·318
13	·128	·259	·394	·538	·694	·870	1·079	1·350	1·771	2·160	2·650	3·012	4·221
14	·128	·258	·393	·537	·692	·868	1·076	1·345	1·761	2·145	2·624	2·977	4·140
15	·128	·258	·393	·536	·691	·866	1·074	1·341	1·753	2·131	2·602	2·947	4·073
16	·128	·258	·392	·535	·690	·865	1·071	1·337	1·746	2·120	2·583	2·921	4·015
17	·128	·257	·392	·534	·689	·863	1·069	1·333	1·740	2·110	2·567	2·898	3·965
18	·127	·257	·392	·534	·688	·862	1·067	1·330	1·734	2·101	2·552	2·878	3·922
19	·127	·257	·391	·533	·688	·861	1·066	1·328	1·729	2·093	2·539	2·861	3·883
20	·127	·257	·391	·533	·687	·860	1·064	1·325	1·725	2·086	2·528	2·845	3·850
21	·127	·257	391	·532	·686	·859	1·063	1·323	1·721	2·080	2·518	2·831	3·819
22	·127	·256	·390	·532	·686	·858	1·061	1·321	1·717	2·074	2·508	2·819	3·792

23	·127	·256	·390	·532	·685	·858	1·060	1·319	1·714	2·069	2·500	2·807	3·767
24	·127	·256	·390	·531	·685	·857	1·059	1·318	1·711	2·064	2·492	2·797	3·745
25	·127	·256	·390	·531	·684	·856	1·058	1·316	1·708	2·060	2·485	2·787	3·725
26	·127	·256	·390	·531	·684	·856	1·058	1·315	1·706	2·056	2·479	2·779	3·707
27	·127	·256	·389	·531	·684	·855	1·057	1·314	1·703	2·052	2·473	2·771	3·690
28	·127	·256	·389	·530	·683	·855	1·056	1·313	1·701	2·048	2·467	2·763	3·674
29	·127	·256	·389	·530	·683	·854	1·055	1·311	1·699	2·045	2·462	2·756	3·659
30	·127	·256	·389	·530	·683	·854	1·055	1·310	1·697	2·042	2·457	2·750	3·646
40	·126	·255	·388	·529	·681	·851	1·050	1·303	1·684	2·021	2·423	2·704	3·551
60	·126	·254	·387	·527	·679	·848	1·046	1·296	1·671	2·000	2·390	2·660	3·460
120	·126	·254	·386	·526	·677	·845	1·041	1·289	1·658	1·980	2·358	2·617	3·373
∞	·126	·253	·385	·524	·674	·842	1·036	1·282	1·645	1·960	2·326	2·576	3·291

N.B.—This table is reprinted from Table III of Fisher and Yates: 'Statistical Tables for Biological, Medical and Agricultural Research, Oliver & Boyd, Ltd., Edinburgh', by permission of the Authors and Publishers.

APPENDIX II.

Distribution of X^2.

Probability.

n	·99	·98	·95	·90	·80	·70	·50	·30	·20	·10	·05	·02	·01	·001
1	$\cdot0^{3}157$	$\cdot0^{3}628$	·00393	·0158	·0642	·148	·455	1·074	1·642	2·706	3·841	5·412	6·635	10·827
2	·0201	·0404	·103	·211	·446	·713	1·386	2·408	3·219	4·605	5·991	7·824	9·210	13·815
3	·115	·185	·352	·584	1·005	1·424	2·366	3·665	4·642	6·251	7·815	9·837	11·341	16·268
4	·297	·429	·711	1·064	1·649	2·195	3·357	4·878	5·989	7·779	9·488	11·668	13·277	18·465
5	·554	·752	1·145	1·610	2·343	3·000	4·351	6·064	7·289	9·236	11·070	13·388	15·086	20·517
6	·872	1·134	1·635	2·204	3·070	3·828	5·348	7·231	8·558	10·645	12·592	15·033	16·812	22·457
7	1·239	1·564	2·167	2·833	3·822	4·671	6·346	8·383	9·803	12·017	14·067	16·622	18·475	24·322
8	1·646	2·032	2·733	3·490	4·594	5·527	7·344	9·524	11·030	13·362	15·507	18·168	20·090	26·125
9	2·088	2·532	3·325	4·168	5·380	6·393	8·343	10·656	12·242	14·684	16·919	19·679	21·666	27·877
10	2·558	3·059	3·940	4·865	6·179	7·267	9·342	11·781	13·442	15·987	18·307	21·161	23·209	29·588
11	3·053	3·609	4·575	5·578	6·989	8·148	10·341	12·899	14·631	17·275	19·675	22·618	24·725	31·264
12	3·571	4·178	5·226	6·304	7·807	9·034	11·340	14·011	15·812	18·549	21·026	24·054	26·217	32·909
13	4·107	4·765	5·892	7·042	8·634	9·926	12·340	15·119	16·985	19·812	22·362	25·472	27·688	34·528
14	4·660	5·368	6·571	7·790	9·467	10·821	13·339	16·222	18·151	21·064	23·685	26·873	29·141	36·123
15	5·229	5·985	7·261	8·547	10·307	11·721	14·339	17·322	19·311	22·307	24·996	28·259	30·578	37·697
16	5·812	6·614	7·962	9·312	11·152	12·624	15·338	18·418	20·465	23·542	26·296	29·633	32·000	39·252
17	6·408	7·255	8·672	10·085	12·002	13·531	16·338	19·511	21·615	24·769	27·587	30·995	33·409	40·790
18	7·015	7·906	9·390	10·865	12·857	14·440	17·338	20·601	22·760	25·989	28·869	32·346	34·805	42·312
19	7·633	8·567	10·117	11·651	13·716	15·352	18·338	21·689	23·900	27·204	30·144	33·687	36·191	43·820
20	8·260	9·237	10·851	12·443	14·578	16·266	19·337	22·775	25·038	28·412	31·410	35·020	37·566	45·315
21	8·897	9·915	11·591	13·240	15·445	17·182	20·337	23·858	26·171	29·615	32·671	36·343	38·932	46·797
22	9·542	10·600	12·338	14·041	16·314	18·101	21·337	24·939	27·301	30·813	33·924	37·659	40·289	48·268

23	10·196	11·293	13·091	14·848	17·187	19·021	22·337	26·018	28·429	32·007	35·172	38·968	41·638	49·728
24	10·856	11·992	13·848	15·659	18·062	19·943	23·337	27·096	29·552	33·196	36·415	40·270	42·980	51·179
25	11·524	12·697	14·611	16·473	18·940	20·867	24·337	28·172	30·675	34·382	37·652	41·566	44·314	52·620
26	12·198	13·409	15·379	17·292	19·820	21·792	25·336	29·246	31·795	35·563	38·885	42·856	45·642	54·052
27	12·879	14·125	16·151	18·114	20·703	22·719	26·336	30·319	32·912	36·741	40·113	44·140	46·963	55·476
28	13·565	14·847	16·928	18·939	21·588	23·647	27·336	31·391	34·027	37·916	41·337	45·419	48·278	56·893
29	14·256	15·574	17·708	19·768	22·475	24·577	28·336	32·461	35·139	39·087	42·557	46·693	49·588	58·302
30	14·953	16·306	18·493	20·599	23·364	25·508	29·336	33·530	36·250	40·256	43·773	47·962	50·892	59·703

For larger values of n, the expression $\sqrt{2\chi^2} - \sqrt{2n-1}$ may be used as normal deviate with unit variance.

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APPENDIX III.

5 Per Cent. Points of e^{2z}.

$n_2 \backslash n_1$	1	2	3	4	5	6	8	12	24	8
1	161·4	199·5	215·7	224·6	230·2	234·0	238·9	243·9	249·0	254·3
2	18·51	19·00	19·16	19·25	19·30	19·33	19·37	19·41	19·45	19·50
3	10·13	9·55	9·28	9·12	9·01	8·94	8·84	8·74	8·64	8·53
4	7·71	6·94	6·59	6·39	6·26	6·16	6·04	5·91	5·77	5·63
5	6·61	5·79	5·41	5·19	5·05	4·95	4·82	4·68	4·53	4·36
6	5·99	5·14	4·76	4·53	4·39	4·28	4·15	4·00	3·84	3·67
7	5·59	4·74	4·35	4·12	3·97	3·87	3·73	3·57	3·41	3·23
8	5·32	4·46	4·07	3·84	3·69	3·58	3·44	3·28	3·12	2·93
9	5·12	4·26	3·86	3·63	3·48	3·37	3·23	3·07	2·90	2·71
10	4·96	4·10	3·71	3·48	3·33	3·22	3·07	2·91	2·74	2·54
11	4·84	3·98	3·59	3·36	3·20	3·09	2·95	2·79	2·61	2·40
12	4·75	3·88	3·49	3·26	3·11	3·00	2·85	2·69	2·50	2·30
13	4·67	3·80	3·41	3·18	3·02	2·92	2·77	2·60	2·42	2·21
14	4·60	3·74	3·34	3·11	2·96	2·85	2·70	2·53	2·35	2·13
15	4·54	3·68	3·29	3·06	2·90	2·79	2·64	2·48	2·29	2·07
16	4·49	3·63	3·24	3·01	2·85	2·74	2·59	2·42	2·24	2·01
17	4·45	3·59	3·20	2·96	2·81	2·70	2·55	2·38	2·19	1·96
18	4·41	3·55	3·16	2·93	2·77	2·66	2·51	2·34	2·15	1·92
19	4·38	3·52	3·13	2·90	2·74	2·63	2·48	2·31	2·11	1·88
20	4·35	3·49	3·10	2·87	2·71	2·60	2·45	2·28	2·08	1·84
21	4·32	3·47	3·07	2·84	2·68	2·57	2·42	2·25	2·05	1·81
22	4·30	3·44	3·05	2·82	2·66	2·55	2·40	2·23	2·03	1·78

23	4·28	3·42	3·03	2·80	2·64	2·53	2·38	2·20	2·00	1·76
24	4·26	3·40	3·01	2·78	2·62	2·51	2·36	2·18	1·98	1·73
25	4·24	3·38	2·99	2·76	2·60	2·49	2·34	2·16	1·96	1·71
26	4·22	3·37	2·98	2·74	2·59	2·47	2·32	2·15	1·95	1·69
27	4·21	3·35	2·96	2·73	2·57	2·46	2·30	2·13	1·93	1·67
28	4·20	3·34	2·95	2·71	2·56	2·44	2·29	2·12	1·91	1·65
29	4·18	3·33	2·93	2·70	2·54	2·43	2·28	2·10	1·90	1·64
30	4·17	3·32	2·92	2·69	2·53	2·42	2·27	2·09	1·89	1·62
40	4·03	3·23	2·84	2·61	2·45	2·34	2·18	2·00	1·79	1·51
60	4·00	3·15	2·76	2·52	2·37	2·25	2·10	1·92	1·70	1·39
120	3·92	3·07	2·68	2·45	2·29	2·17	2·02	1·83	1·61	1·25
∞	3·84	2·99	2·60	2·37	2·21	2·09	1·94	1·75	1·52	1·00

Lower 5 per cent. points are found by interchange of n_1 and n_2, *i.e.*, n_1 must always correspond with the greater mean square.

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APPENDIX III.

Variance Ratio—(cont.)

1 Per Cent. Points of e^{2z}.

n1 / n2	1	2	3	4	5	6	8	12	24	∞
1	4052	4999	5403	5625	5764	5859	5981	6106	6234	6366
2	98·49	99·01	99·17	99·25	99·30	99·33	99·36	99·42	99·46	99·50
3	34·12	30·81	29·46	28·71	28·24	27·91	27·49	27·05	26·60	26·12
4	21·20	18·00	16·69	15·98	15·52	15·21	14·80	14·37	13·93	13·46
5	16·26	13·27	12·06	11·39	10·97	10·67	10·27	9·89	9·47	9·02
6	13·74	10·92	9·78	9·15	8·75	8·47	8·10	7·72	7·31	6·88
7	12·25	9·55	8·45	7·85	7·46	7·19	6·84	6·47	6·07	5·65
8	11·26	8·65	7·59	7·01	6·63	6·37	6·03	5·67	5·28	4·86
9	10·56	8·02	6·99	6·42	6·06	5·80	5·47	5·11	4·73	4·31
10	10·04	7·56	6·55	5·99	5·64	5·39	5·06	4·71	4·33	3·91
11	9·65	7·20	6·22	5·67	5·32	5·07	4·74	4·40	4·02	3·60
12	9·33	6·93	5·95	5·41	5·06	4·82	4·50	4·16	3·78	3·36
13	9·07	6·70	5·74	5·20	4·86	4·62	4·30	3·96	3·59	3·16
14	8·86	6·51	5·56	5·03	4·69	4·46	4·14	3·80	3·43	3·00
15	8·68	6·36	5·42	4·89	4·56	4·32	4·00	3·67	3·29	2·87
16	8·53	6·23	5·29	4·77	4·44	4·20	3·89	3·55	3·18	2·75
17	8·40	6·11	5·18	4·67	4·34	4·10	3·79	3·45	3·08	2·65
18	8·28	6·01	5·09	4·58	4·25	4·01	3·71	3·37	3·00	2·57
19	8·18	5·93	5·01	4·50	4·17	3·94	3·63	3·30	2·92	2·49
20	8·10	5·85	4·94	4·43	4·10	3·87	3·56	3·23	2·86	2·42
21	8·02	5·78	4·87	4·37	4·04	3·81	3·51	3·17	2·80	2·36
22	7·94	5·72	4·82	4·31	3·99	3·76	3·45	3·12	2·75	2·31

23	7·88	5·66	4·76	4·26	3·94	3·71	3·41	3·07	2·70	2·26
24	7·82	5·61	4·72	4·22	3·90	3·67	3·36	3·03	2·66	2·21
25	7·77	5·57	4·68	4·18	3·86	3·63	3·32	2·99	2·62	2·17
26	7·72	5·53	4·64	4·14	3·82	3·59	3·29	2·96	2·58	2·13
27	7·68	5·49	4·60	4·11	3·78	3·56	3·26	2·93	2·55	2·10
28	7·64	5·45	4·57	4·07	3·75	3·53	3·23	2·90	2·52	2·06
29	7·60	5·42	4·54	4·04	3·73	3·50	3·20	2·87	2·49	2·03
30	7·56	5·39	4·51	4·02	3·70	3·47	3·17	2·84	2·47	2·02
40	7·31	5·18	4·31	3·83	3·51	3·29	2·99	2·66	2·29	1·80
60	7·08	4·98	4·13	3·65	3·34	3·12	2·82	2·50	2·12	1·60
120	6·85	4·79	3·95	3·48	3·17	2·96	2·66	2·34	1·95	1·38
∞	6·64	4·60	3·78	3·32	3·02	2·80	2·51	2·18	1·79	1·00

Lower 1 per cent. points are found by interchange of n_1 and n_2, *i.e.*, n_1 must always correspond with the greater mean square.

APPENDIX IV

Gene symbols for paddy, cholam, and cotton are given here for easy reference.

PADDY.	*Symbols.*
Apiculus—	
Purple or shades : colourless ...	**Ap_1 : Ap_6**
Anthocyanin—	
presence : absence	**A : a**
Diluter of anthocyanin	**Di : di**
Auricle—	
Presence : absence	**Au : au**
Purple : non-purple	**Aup_1 : aup_1**
	Aup_2 : aup_2
Awning—	
Fully awned : partly awned : awnless	**An_3 : an_3**
	An_4 : an_4
Fully : mostly : rarely : awnless	**An_1 : an_1**
	An_2 : an_2
Awnless : awned	**Ian : ian**
Awn colour—	
Black : Reddish brown	**Anb : Anbr**
Red : colourless	**Anr : anr**
Brown : colourless	**Anbr : anbr**
Purple : colourless	**Anp : anp**
Purple : red	**Anp : Anr**
Chlorophyll deficiencies—	
Green : albino	**W_1 : w_1**
	W_2 : w_2
	W_3 : w_3
Green chlorina	**Chl : chl**
Green lutescent	**L : l**
Green lethal yellow	**Y_1 : y_1**
	Y_2 : y_2
Green tip burn yellow	**Tp_a : tp_a**
	Tp_b : tp_b
Green variegated	**Vr : vr**
Green virescent yellow	**V_1—V_5**
virescent white	**v_1—v_5**
	VJ_1—vj_1
Coleoptile colour—	
Purple : no colour	**Cp : cp**

Disease reaction—	
(*Cercospora Oryzæ*)	
Resistance : susceptible	Ce_1—Ce_4
	ce_1—ce_4
	Ce_a : ce_a
(*Leptosporium salvini Cattaneo*)	Ce_b : ce_b
Resistance : susceptible	Le : le
(*Piricularia oryzæ*)	
Resistance : Susceptible	Pi_a : pi_a
	Pi_b : pi_b
Dwarfing of plants—	
Non-dwarf : dwarf ...	D : d
Non-dwarf : dwarf Japan I	D_1 : d_1
Non-dwarf : dwarf Japan II	D_2 : d_2
Non-dwarf : dwarf kolamba	D_3 : d_3
Non-dwarf : dwarf Y 2139	D_4 : d_4
Non-dwarf : dwarf Bunketuto	D_5 : d_5
Dwarf : non-dwarf ...	Id : id
Endosperm character—	
Starchy : glutinous ...	Wx : wx
Vitreous : opaque ...	Op : op
Vitreous : white belly ...	Wb : wb
Flowering—	
Late : early	Fl_1 : fl_1
	Fl_2 : fl_2
	Fl_a : fl_a
	Fl_b : fl_b
Early : intermediate : late	Ifl : ifl
Glume colour—	
Purple : non-purple ...	Gp_a : gp_a
	Gp : gp_b
Red : colourless ...	Gr_a : gr_a
	Gr_b : gr_b
Glume size—	
Short : long	G_1 : g_1
	G_2 : g_2
Growth habit—	
Geotropic : ageotropic ...	La : la
Erect : prostrate ...	Er : er
Erect : floating ...	Ef_1 : ef_1
	Ef_2 : ef_2
Spreading : erect ...	Es : Esr
Height—	
Tall : short	T : t
Short : tall	It : it

Internode colour—		
Light brown : colourless	...	**Ntbr : ntbr**
Light purple : colourless	...	**Ntr : ntr**
Purple : colourless ...	...	**Ntp : ntp**
Purple lining : colourless	...	**Ntv : ntv**
Juncture colour—		
Purple : non-purple ...	...	**Jp_1 : jp_1** **Jp_2 : jp_2**
Leaf blade—		
Normal : rolled ...	...	**Lro : lro**
Normal : twisted ...	...	**Ltw : ltw**
Leaf blade colour—		
Green : purple ...	...	**Ilp : ilp**
Purple : green ...	...	**Lp : lp**
Purple : purple striped : green	...	**Lp : Lv**
Leaf margin—		
Coloured : colourless ...	...	**Lmp : lmp**
Leaf sheath—		
Coloured : colourless ...	...	**Lsp_1 : lsp_1** **Lsp_2 : lsp_2**
Purple : striped : green...	...	**Lsp : Lsv : green.**
Lemma and Palea shelling—		
Easy : touch shelling ...	...	**Itf : itf**
Tough : easy shelling ...	...	**Tf : tf**
Normal : parted lemma and palea		**Hpt : hpt**
Lemma and palea colour—		
Colourless : gold ..	..	**Hg : hg**
Ligule—		
Presence : absence ...	...	**Lg : lg**
Ligule colour—		
Coloured : colourless ...	...	**Lgp : lgp**
Node colour—		
Purple : green ...	...	**Np : np**
Panicle density—		
Lax : dense	...	**Lx_1 : lx_1**
Non-spreading : spreading	...	**Spr_a : spr_a** **Spr_b : spr_b**
Panicle exsertion—		
Partly emerged : tip emerged	..	**Ex_1 : Ex_3**
Tip enclosed	..	**ex_1 : ex_3**
Peduncle shape—		
Normal : sinuous ...	..	**Ne_1 : ne_1** **Ne_2 : ne_2**

Pericarp colour—

Black : intermediate : white	Prp : prp
Brown : white	Pbr : pbr
Red : white	Pr_1 : pr_1
	Pr_2 : pr_2

Pistil number—

One : many	Mp : mp

Root colour—

Purple : white	Rp : rp

Scent—

Scented : non-scented	O_a : o_a
	O_b : o_b
	O_c : o_c

Spikelet arrangement—

Non-clustered : clustered	Cl : cl

Spikelet attachment—

Shattering : non-shattering ...	Sh_1 : sh_1
	Sh_2 : sh_2
Non-shattering : shattering ...	Ish : ish

Spikelet length—

Short : (intermediate) : long ...	Kl : kl
Short : medium	Km : km

Spikelet shape—

Round : oval	Kr_a : kr_a
	Kr_b : kr_b

Sterility—

Fertile : awned sterile	Fan : fan
Fertile : barren sterile	Fb : fb
Fertile : completely sterile ...	Fo : fo
Fertile : male sterile	Fm : fm
Fertile : paleaceous sterile ...	Fp : fp
Fertile : semi sterile	Fs : fs
Fertile : slender semi sterile ...	Fsl : fsl
Fertile : staminoidal sterile ...	Fst : fst
Fertile : sterile (shrivelled stamens)	Fsh : fsh
Fertile : sterile (degeneration of pistil)	Fdp : fdp
Fertile : female sterile	Ffs : ffs

Stigma colour—

Colourless : coloured	Sp_1 : sp_1
	Sp_2 : sp_2
Purple : white	Sp_a : sp_a
	Sp_b : sp_b

Stem lodging—

Lodging : non-lodging	Ld : ld
Normal : brittle	Be : be

Miscellaneous—

Green : stunted yellow	Sty : sty

CHOLAM (Sorghum species).

Coleoptile—	
Red: green ...	R : r
Purple : green ...	Pc : pc
Stem—	
Red: green ...	Rs : rs
Chlorophyll—	
Normal green : white	W_1—W_4 w_1—w_4 W_5—W_{12} w_5 : w_{12}
Normal : virescent white	V_1—V_8 : v_1—v_8
Normal : yellow .	Y_1—Y_6 : y_1—y_6
Normal : pale green lethal	Pg_1—Pg_3 : pg_1—pg_3
Normal : Xantha .	Cl : cl
Normal : patchy albino .	Y_x : y_x
Normal : banded .	Alp : alp
Normal : patchy pale	Cb : cb
Blush green : glossy green	Cbl : cbl
Seedling—	
Late purple : green	Pls : pls
Plant colour—	
Purple (leaf sheath : Brown and glume)	P : p
Reddish purple : blackish purple ...	Q : q
Green internode : brownish purple	Mtb : mtb
Green stem and leaves : Red ...	Cr : cr
Green stem and leaves : yellow ...	Cy_1—cy_2 : cy_1—cy_2
Green stem and leaves : golden ...	Cg : cg
Pithy : juicy	D : d
Insipid : sweet	X—x
Bloom present : absent	Bm : bm
Bloom heavy : sparse	H : h
Nodal band—	
Purple : green	Pj : pj
Reticulated purple : green ...	Nr : nr
Hairy : glabrous	Nh : nh
Leaf—	
Dark green : light green	C_1—C_2 : c_1—c_2
Normal : yellow	Y_1 : y_1

Normal : fired	$F_1 : f_1$
Normal : zebra	Z : z
Normal : green striped	Gs : gs
Normal : striped (longitudinal) ...	Cs : cs
Wavy : flat	Mu : mu
Margin non-drying : drying ...	Md : md
Tip hairy : glabrous	Lh : lh
Mid-rib normal : weak	Md : md
Mid-rib yellow : non-yellow ...	$Y_{md} : y_{md}$
Mid-rib hairy : hairless edges ..	Mdh : mdh
Junction—	
Present and ligulate : absent and ligulate	Lg : lg
Smooth : corrugated	Jc : jc
Junction and Node—	
Purple : green	Pj : pj
Panicle—	
Peduncle straight : wavy	Wy : wy
Loose : compact	$Pa_1 : pa_1$
Pulvinate and divergent secondary branches epulvinate and adpressed	$Pa_2 : pa_2$
Pulvinus purple : no purple	Px : px
Normal tip : sterile tip	Pats : pats
Spikelets—	
Purple hairs : hyaline hairs	Ph : ph
Non-shedding : shedding	Sh : sh
Pedicelled—	
Persistent : shedding	$Sh_1 : sh_1$
Purple wash : green	Pw : pw
Glume—	
Purple at emergence : no purple	Gep : gep
Coriaceous : papery	Py : py
Purple (mature) : no purple	P : p
Red (mature) : no red (black)	Q : q
Red : Black	Gb : gb
Black (mature) : Red	Gr : gr
Black (mature) : Straw colour	Gs : gs
Deep coloured : dilute	Cd : cd
Bleached : deep coloured	Ci : ci
Edges not rolled in : Edges rolled in	Gx : gx
Hairy : glabrous	Gh : gh
Long hairs : short hairs	Gf : gf
Awn—	
Awnless : awned	A : a
Awnless : tip awned	$A : a_t$
Constant : inconstant length of awn	Ai : ai
Purple tip : no purple	Ap : ap

Anther—	
Normal : antherless	**Al : al**
Normal : empty	**Ms : ms**
Normal : empty pollen	**Me : me**
Anther (fresh)—	
Yellow : purple blotched ...	**As : as**
Purple base : no purple ...	**Ab : ab**
Purple : Yellow	**Pan : pan**
Anther (dry)—	
Brick red tan : tan	**R : r**
Red : no red	**R : r**
Brown : sienna	**B_1—B_2 : b_1—b_2**
Anther filament—	
Normal length : reduced ...	**Fr : fr**
Stigma—	
Purple : no purple ...	**Ps : ps**
Feathers bushy : sparse	**Sp : sp**
Fully feathered : basal feathered ..	**Stbf : stbf**
Hairy style awn columns barbed : smooth and awn column smooth	**Bc : bc**
Seed—	
Pericarp yellow : white	**Y : y**
Pericarp red : no red	**R : r**
Pericarp brown : no brown ...	**B_1—B_2 : b_1—b_2**
Pericarp intensified : light...	**I : i**
Pericarp whole coloured : base only coloured	**W : w**
Wash on pericarp : no wash	**M : m**
Purple blotched : no purple	**Pb : pb**
Purple tip : no purple	**Pgt : pgt**
Shape umbonate : round top	**U : u**
Normal : dimpled grain	**Dp : dp**
Pearly : chalky	**Z : z**
Thick (mesocarp) : thin (mesocarp) ...	**S : s**
Nucellar layer present : absent	**B : b**
Endosperm starchy : sugary	**Su : su**
Endosperm starchy : waxy	**Wx : wx**
Non-scented : scented	**Sc : sc**
Single : double	**Co : co**
Double : single	**Ts : ts**
Plant height and duration—	
Tall : normal	**T : t**
Standard : dwarf	**D_1 : d_1**
Dwarf : doubles dwarf	**D_2 : d_2**

Standard (broom corn) : Japanese dwarf	**D : d**
Short early (Durra) : Tall late	$\mathbf{In_1 : in_1}$
Late : early	**E : e**

Habit—

Spreading : erect	**So : so**
Tillering : single stalked	**Tx : tx**
Delayed : uniform tillering	**Tu : tu**
Normal : midget	**M : m**
Normal : tiny	**Inty : inty**

Disease resistance—

Smut resistant : susceptible	**R : r**
Susceptible : resistant	**K : k**
Susceptible : resistant	**S : s**
Resistant : susceptible (feterita)	**B : b**

ASIATIC COTTONS (2n—26).

Chlorophyll deficiency—

Green : chlorophyll deficient	**Chl : chl**
Green : virescent yellow	$\mathbf{V_1 : v_1}$
Crumpled : Normal	$\mathbf{Cp_a : cp_a}$
	$\mathbf{Cp_b : cp_b}$
Curly : non-curly	**Cu : cu**

Leaf shape—

Mutant broad : broad	$\mathbf{L^B : l}$
Mutant intermediate : broad	$\mathbf{L^I : l}$
Laciniated : broad	$\mathbf{L^L : l}$
Narrow : broad	**L : l**

Leaf nectaries—

Present : absent	**Ne : ne**

Anthocyanin (*spotted series*)**—**

Red plant body : green	$\mathbf{R^{rs}{}_2 : R^{os}{}_2}$
Red leaf green	$\mathbf{R^{ls}{}_2 : R^{os}{}_2}$
Calyx red : green	$\mathbf{R^{cs}{}_2 : R^{cs}{}_2}$
Tinged stem : green	$\mathbf{R^{as}{}_2 : R^{os}{}_7}$

(*spotless series*) :

Red leaf	$\mathbf{R_2{}^{LO}}$
Tinged stem	$\mathbf{R_2{}^{AO}}$
Duplicate	$\mathbf{R_2{}^{GO}}$
Spot reducer	**Yr**

Corolla colour—

Yellow petal : white	$\mathbf{Y_a{}^p : y_a{}^p}$
Pale white	$\mathbf{Y_a{}^p : y_a{}^p}$
Pale complementary	$\mathbf{Y_b{}^p : y_b{}^p}$
Pale complementary	$\mathbf{Y_c{}^p : y^a}$
Yellow depressor	**Ydb**

Pollen colour—

Yellow : pale cream	**P_a—P_b** **p_a—P**

Meristic variation—

Increase in no. of floral part : normal	**M : m**

Sterility—

Fertile : sterile	**Stp : stp**
Fertile : female sterile	**Stg : stg**

Petaloidy—

Normal : petaloid	**Pdy : pdy**

Boll dehiscence—

More : less	**De : de**

Lint colour—

Khaki : white	**Lc_1^k : lc_1**
Khaki duplicate : white	**L^k : lc_1**
Light brown : white	**$Lc^B{}_2$: lc_2**
Light brown : white (duplicate)	**L^Bc_3 : lc_3**

Lintlessness—

Hairy linted	glabrous (complementary)	**H_a : H_b**
Hairy linted	Hairy lintless (complementary)	**L^{ia} : L_{ib}**
Hairy linted	Hairy lintless (sometimes lethal)	**L_{ic} : l_{ic}**

NEW WORLD COTTONS (2n—52).

Chlorophyll deficiency—

Green : chlorophyll deficient	**Chl_1—Chl_2**
Green : Irrescent yellow	**V : v**

Crinkled dwarf—

normal : crinkled dwarf	**Cr : cr**

Habit—

Normal : cluster habit	**Cl : cl**
Long : short fruiting branches	**Sh : sh**

Leaf shape—

Super okra : normal	**L^s : l**
Okra : normal	**L^o : l**

Anthocyanin (*spotted series*)—

Red leaf	**R_2^{LW}**
Tinged stem	**R_2^{AS}, R_2^{AL}** **R_2^{AF}**
(*spotless series*).	
Tinged stem	**R_2^{AO}**
Duplicate red spotless	**R_1^{RO}**

Corolla colour—

Yellow petal	Y_1
Pale	Y_1^p

Pollen colour—

Yellow and cream	P

Lint colour—

Khaki : white duplicate	$L_{c1}^k : lc_1$
	$L_{c2}^k : lc_2$
Green : white	Lg : lg

Seed fuzz—

Naked : fuzzy	Fn : fn
Tufted : naked (Peruvian)	Ft : ft
Less fuzzy : More fuzzy (Peruvian)	Fm : fm
Tufted : fuzzy (upland)	Fz : fz

Seed fuzz colour—

Green : white	Fgr : fgr
Brown : white	Fbr : fbr

APPENDIX V

CHROMOSOME NUMBERS

A

Acacia arabica	52, 104
A. baileyana	26
A. dealbata	26
A. decurrens	26
A. farnesiana	52
A. horrida	52, 104
Aeschynomene indica	40
Aegilops caudata	14
A. cylindrica	28
A. ovata	28
Agave americana	20
A. virginia	24
Ageratum conyzoides	20
Alisma plantago	12
Allium cepa	16
A. cernuum	16
A. fistulosum	16
A. sativum	16
Aloe grandis	14
Alpinia allughas	48
A. galanga	48
A. nutans	48
A. vittata	48
Andropogon annulatus	40
A. caesium	22
A. caricosus	50
A. elliottii	20
A. foviolatus	45
A. furcatus	70
A. gryllus	40
A. guianensis	32
A. halepensis. (See *Sorghum halepense*)	40
A. intermedius	70
A. ischaemum	35
A. monticola	36
A. nardus	20
A. nutans	40
A. piptatherus	40
A. pumilus	40
A. purpereo sericens	40
A. saccharoides	60
A. scoparius	40
A. sorghum	20
A. sorghum var. sudanensis	20
A. versicolor	10
A. virsinicus	20
Anhenatherum elatius	28
Anthoxanthum aristatum	10
A. odoratum	10, 20
Antigonon leptopus	40
Antirrhinum majus	16
Apluda mutica	20, 40
Aquilegia vulgaris	14
Arachis hypogaea	40
A. nambyquare	40
A. prostrata	40
A. rasteiro	40
Aristida adscensions	22
Artemesia vulgaris	18
Arundinaria fortunei	48
Atropa belladonna	72
Avena abyssinica	28
A. algeriensis	42

A

A. barbata	28
A. brevis	14
A. bruhusiana	14
A. byzantina	42
A clauda	14
A. fatua	42
A. ludoviciana	42
A. nuda	42
A. nudibrevis	14
A. orientalis	42
A. sativa	42
A. sterilis	42
A. strigosa	14
A. wiestii	14

B

Balanophora elongata .	16
B. japonica	94, 112
B. vulgaris	18
B. vulgaris var. perennis ...	18
Bixa orellana	14
Brachiaria erucaeformis ...	18
B. mutica . ..	36
Brassica auriculata	20
B. campestris	20
B. carinata	34
B. juncea	36
B. napus	20
B. nigra	16
B. oleracea (and derivatives) ...	18
Briza maxima	14
B. media	14
B. minor	10
Bryonia alba	20
B. dioica	20
Bryophyllum calycinum ...	40

Cadaba indica	18
Cajanus cajan	22
Camellia sinensis	30
Canavalia ensiformis .. .	22
Canna indica	6, 16, 18, etc.
Cannabis gigantea	20, 40
C. sativa	20
C. sativa var. kif.	20, 40
C. sativa var. communis	20, 40
Capparis acutifolia	84
C. cynophallophora .. .	18
C. sepiaria	40
C. Rothii	40
C. zeylanica	40
Capsicum annuum	24
Carica papaya	18
Carthamus tinctorius (Pusa types) .	24
Cassia auriculata (from Waltair) .	28
,, *(from Ceylon)* .	14, 16
C. dimidiata	16
C. fistula	24
C. mimosoides	16, 32, 48
C. occidentalis	26
C. tomentosa	24
C. tora	26
Casuarina equisetifolia .. .	24
C. montana	24
C. quadrivalvis	16, 24
C. stricta	24
Cenchrus catharticus	34

C

C. ciliaris	36
C. echinatus	34
C. inflexus	34
C. mysuroides	70
C. tribuloides	34
Ceratophyllum demersum	24
C. submersum	24
Cercis siliquastrum	14
Chenopodium album	18
Chloris barbata	20, 40
C. bourneii	50
C. caudata	40
C. cucullata	40
C. distichophylla	20
C. gayana	20
C. gracilis	30
C. submutica	80
C. truncata	40
Chrysanthemum alpinum	36
C. Carinatum	18
C. cinaerifolium	18
C. coccineum	18
C. coronarium	18
C. indicum	36
C. japanicum	18
C. marginatum	90
C. segetum	18
Cicer arietinum	14
C. arietinum (Kabuli type)	16
C. gigas (a mutant)	16
C. pinnatifidum	16
C. songaricum	14
Citrullus vulgaris	22
Clematis paniculata	16
Cleome chelidonii	34
C. gigantea	70
C. gigantea var. gigas	140
C. paradoxa	32
C. spinosa	20
C. viscosa	20
Clitoria ternatea	16
Coccinia indica	26
C. hirtella	24
Cocos nucifera	32
Coffea arabica	22
C. liberica	22
Coix lachryma-jobi	20
Coleus aromaticus	32
C. rehneltianus	48
Corchorus capsularis	14
C. oletorius	14
Costus discolor	18
C. igenus	18
C. speciosus	36
Crataeva religiosa	26
Crocus sativus	24
Crotalaria alata	16
C. anagyroides	16
C. arenaria	16
C. argyraea	16
C. incana	14
C. juncea	16
C. laburnifolia	16
C. medicaginea	16
C. mysorensis	16
C. obovata	16
C. orixensis	16
C. quinquefolia	16
C. retusa	16
C. sericea	16

C. striata ...	16
C. trifoliastrum ...	16
C. usaramoensis ...	16
C. valetonii ...	16
C. verrucosa ...	16
Cucumis maxima ...	48
C. melo ...	24
C. sativus ...	14
C. moschata ...	40
C. pepo ...	40
Cyamopsis psoralioides	14
Cymbopogon nardus	20
Cynodon dactylon ...	36

D

Dactylis glomerata ...	28
D. aegyptium ...	48
Dactyloctenium scindicum	48
Dahlia imperialis ...	32
Datura fastuosa ...	24
D. ferox ...	24
D. stramonium ...	24
Delphinium chinense	16
D. hybridum ...	32
D. speciosum ...	16
Dendrocalamus strictus	72
Desmodium grandiflorum	22
Digitalis purpurea ...	56
Digitaria exilis ...	54
Dinebra arabica ...	20
D. retroflexa ...	20
Diospyros Kaki ...	90
Dolichos biflorus ...	24
D. lablab ...	22, 24
D. multiflorus ...	24
D. niloticus ...	22
D. ornatus ...	22
Drosera longifolia ...	40
D. rotundifolia ...	20

Echinochloa crus-galli	42
E. frumentacea Church	42
Avdulov	54
Hunter	36
Ehrharta calycina ...	48
E. erecta ...	24
E. longiflora ...	48
E. Panicea ...	24
Eicchornia crassipes...	32
Elettaria cardamomum	48
Eleusine brevifolia ...	36
E. coracana ..	36
E. flagellifera ...	45
E. focussa ...	39
E. indica ...	18
E. oligostachya ...	18
E. tristachya ...	18
Eragrostisabyssinica	40
E. alvida ...	40
E. aspera ...	20
E. cilianesis ...	20
E. Japonica ...	20
Erythrina cristagalli	44
Euchlaena mexicana	20
Eupatorium galandulosum	51
Euphorbia pulcherrima	

I

I. parviflora	14
I. pseudotinctoria	16
I. sessiliflora	32
I. suffruticosa	32
I. viscosa	16
Iseilema anthephoroides	68

J

Juglans californica	34
J. regia	32

K

Kaempferia galanga	54
K. Gibsoni	24
K. Gilbertii	36
K. rotunda	54

L

Lathyrus angulatus	14
L. annuus	14
L. aphaca	14
L. articulatus	14
L. cicera	14
L. cirrhosus	14
L. latifolius	14
L. ochroleucas	14
L. odoratus	14
L. pubescens	14
L. sativus	14
Lens esculenta	14
Leptochloa chinensis	40
L. polystachya	20
Linum alpinum	18
L. angustifolium	30
L. hirsutum	16
L. perenne	18
L. punctatum	18
L. strictum	18
L. tenuifolium	18
L. usitatissimum	30
Litchi chinensis	28
Lolium perenne	14
Lupinus albus	50
L. luteus	46, 48, 52
L. sativus	44, 45

M

Magnolia parviflora	38
Matthiola incana	14
Medicago apiculata	46, 16
M. arabica	16
M. arborea	32
M. carstiensis	16
M. cillaris	16
M. Coronata	16
M. denticulata	16
M. disciformis	16
M. dyawakhetica	16
M. echinus	16
M. falcata	16, 32
M. gerardi	16
M. glutinosa	32
M. helix	16
M. hemicycla	32
M. hispida	14
M. intertexta	16

M

M. laciniata	16
M. lappacea	16
M. littoralis	16
M. lupulina	16
M. maculata	16
M. marina	16
M. media	32, 35
M. minima	16
M. murex	16
M. muricata	16
M. nigra	16
M. oliviformis	16
M. orvicularis	16
M. ovalis	32
M. platycarpa	16
M. radiata	16
M. rotata	16
M. ruthenica	16
M. sativa	32
M. scutellata	32
M. solcirollii	16
M. sphaerocarpa	16
M. tenoreana	16
M. tornata	16
M. tribuloides	16
M. truncatula	16
M. tuberculata	16
M. turbinata	16
Melilotus alba	16
M. altissima	16
M. caspia	16
Melilotus dentata	16
M. gracilis	16
M. indica	16
M. officinalis	16
M. segetalis	16
M. speciosa	16
M. suaveolens	16
M. sulcata	16
M. wolgica	16
Melinis minutiflora	36
M. spicata var lampreilema	36
Mentha piperita	36
M. sylcestris	18
Merua arennia	20
Microlaena stipoides	48
Mimosa pudica	48
Mirabilis Jalapa	58
M. tubiflora	32
Morus alba	28
M. indica	28
M. rotundifolia	28
Muhlenbeckia platyclados	20
Musa cavendishii	33
M. rosacea	22
M. sanguinea	22
M. sapientum var Gros michel	33
M. zebrina	22

N

Nardus stricta	26
Nelmbium luteum	16
Nicotiana bigelovii	48
N. glauca	24
N. glutinosa	24
N. langsdorfii	18
N. longiflora	20
N. nudicaulis	48
N. paniculata	24

N

N. plumbaginifoial	20
N. rusbyi	24
N. rustica	48
N. sylvestris	24
N. tabacum	48
Nymphaea alba	84
N. lotus	56
N. tuberosa	84

O

Ononis biflora	32
O. fruticosa	32
Oplismenus burmanii	72
Ornithopus sativus	14, 16
Orobanche minor	38
Oryza barthii	24
O. coarctata	48
O. cubensis	24
O. latifolia	48
O. sativa	24
Oryzopsis miliacea	24
O. virescens	24

P

Panicum acroanthum	36
P. altissimum	60
P. bulbosum	70
P. californicum	18
P. capillare	18
P. colonum	130
P. dichotomiflorum	54
P. disatchyum	36
P. eruciforme	18
P. esculentum	54, 58
P. exile	54
P. fluitans	(*more than*) 100
P. isachne	18
P. lindheimeri	16, 18
P. miliaceum	36
P. miliare	36
P. muticum	36
P. plicatum	36
P. repens	40
P. sanguinale	36
P. seribnerianum	18
P. sphaerocarpon	18
P. subvillosum	14, 18, 20
P. teneriffe	40
P. tsuge orium	18
P. tuberculatum	18
Panicum verticillatum	20
P. virgatum	80
Papaver somniferum	22
Paspalum dilatatum	40, 50
P. lanceolatum	40
P. lentiferum	45
P. membranaceum	25
P. muehlenbergli (*P. pubescens*)	18, 20, 22
P. quadreferum	60
P. scrobiculatum	40
P. setaceum	50
P. stoloniferum	20
P. tenellum	55
P. virgatum	40, 80
Pennisetum clandestinum	36
P. compressum	14
P. glaucum	14
P. longistylum	45

P

P. macrourum	45
P. orientale	36
P. ruppelii	27
P. setosum	54
P. typhoides	14
P. villosum	45
Phalaris arundinacea	14, 28
P. caerulescens	14
P. canariensis	12, 28
P. lemmoni	14
P. minor	28
P. paradoxa	14
P. tuberosa	28
Phaseolus aconitifolius	22
P. acutifolius	22
P. angularis	22
P. aureus	22
P. capensis	22
P. chrysanthos	22
P. lunatus	22
P. multiflorus	22, 24
P. mungo	22, 24
P. nigerrimus	22
P. radiatus	22, 24
P. radiatus var curea	22
P. radiatus var flexuosus	22
P. trilobus	24
P. vulgaris	22
Phleum pratense	42
Phoenix dactylifera	36
P. sylvestis	36
Phragmites communis	54, 36, 48, 96, 42
Physalis peruviana	24, 48
Piper betle var hispidula	32
P. subpeltatum	24
Pisum arvense	14
P. elatius	14
P. fomardi	14
P. fulvum	14
P. humile	14
P. satiaum	14
Plantago indica	12
Polygonum compactum	44
P. orientale	22
P. plebejum	40
P. virginianum	44
Portulaca grandiflora	18
Primula floribunda	18
P. kewensis	36
P. verticillata	18
Pyrus communis	34, 51
P. communis var. Alexander Lucas	46
P. elaeagnifolia	34
P. malus	34
P. malus var. Canadian Reinette	15
P. malus var. Delicious	28
P. sinensis	34

Q

Quercus cerris	24
Q. coccinea muereh	24
Q. coccinea wangg	24
Q. glandulifera	24, 22
Q. nigra	24, 22

R

Raphanus sativus	16
Rhoeo discolor	16

R

Ribes americana	12
R. nigram	16
R. orientale	16
R. rubrum	16
Ricinus communis	20
R. zanzibarensis	20
Rosa arvensis	14
R. cania	16, 35
R. indica	14
R. pimpinellifolia	26

S

Sacenarum officinarum	80
S. spontaneum	48
Indian forms Dehra Dun	56
Coimbatore	64
Puri, Chittan	80
Java form from Sumatra ...	128
Sagitaria sagittefolia	16
Sanseveiria cylindrica	102, 104
S. zeylanica	40, 42
Schilla indica	44, 46
Secale africanum	14, 15, 16
S. cereale	12, 14
,, *winter rye*	14, 16
,, *summer rye*	14, 16
Sesamum orientale	26
S. prostratum	32
S. radiatum	64
Sesbania aculeata	32
S. grandiflora	14
S. etaria glauca	36
S. vitalica	18
S. verticillata	36
S. ridis	18
Siaipis alba	24, 18
S. arvensis	24
Solanum acaule	48
S. ajanhuiri	24
S. ajuscosee	48
S. andigennum	48
S. antipoviczii	48
S. aracc-papa	24
S. brevidens	24
S. bukasovii	24
S. caldasii	24
S. caldasii glabrascens	24
S. cardiophyllum	36
S. chacoense	24
S. chaucha	36
S. choccla	36
S. colombianum trianae	48
S. coyacanum	36
S. cuencanum	36
S. curtilobum	60
S. demissum	72
S. diphyllum	72
S. edinense	48, 60
S. fastigiatum	72
S. fernandezianum	24
S. fendleri	48
S. goniocalyx	24
S. jamiesii	24
S. juzepezukii	36
S. kesselbrenneri	24
S. leptostigma	48
S. looserii	24
S. magli	36
S. mammilliferum	36

S

S. medians	36
S. melongena	24
S. nigrum	72
S. nigrum var gigas	144
S. phureja	24
S. polyadenium	24
S. riobambense	36
S. rybinii	24
S. semidemissum	60
S. stenotomum	24
S. tenuifilamentum	36
S. tuberosum	48
S. vallis mexici	36
S. vavilovii	24
Sorghum effusum	20
S. drummondii	20
S. durra	20
S. halepense	40
S. hewisonii	20
S. versicolor	10
S. verticilliflorum	20
S. virgatum	20
Spartina alterniflora	70
S. stricta	56
S. townsendii	126
Spergula arvensis	18
Spinacea oleracea	12
Sporobolus diandrus	36
S. indicus	18, 36
Stipa pulcherrima	44

T

Tamarindus indica	24
Tecoma tagliabuana	40
Tephrosia hookeriana	32
Thaliotrum javanicum	42
T. orientale	42
T. tuberosum	28
Thea sinesis	30
Themeda arguens	20
T. triandra	60
Theobroma cacao	16
Thespesia populnea	16, 20, 26
Tragus racemosus	40
Trifolium aureum	14
T. dubium	28
T. glomeratum	14, 16
T. incarnatum	14, 16
T. involucratum	28
T. pratense	14
T. campestre	14
T. resupinatum	16
Trigonella foenumgraecum	16
Triticum acuminatum	28
T. aegilopoides	14
T. albidum	42
T. compactum	42
T. dicoccoides	28
T. dicoccum	28
T. durum	28
T. macha	42
T. monococcum	14
T. orientale	28
T. persicum	28
T. polonicum	28
T. pyramidale	28
T. spelta	42
T. sphaerococcum	42
T. thaoudar	14

APPENDIX VI

GLOSSARY

Acclimatisation—Inuring plants to new climate.

Acentric—Whole or part of a chromatid or chromosome without centromere.

Acquired character—Variation or modification of a character arising from the influences of environmental factors during the development of the organism.

Albinism—Absence of chlorophyll producing an albino. This is due to genetic causes. This is in contrast to chlorosis or etiolation caused by environmental factors.

Allelomorph—(allele) One of the contrasting pair of factors which are located on corresponding loci of homologous chromosomes.

Allopolyploid—A polyploid derived by doubling of chromosomes in hybrids.

Allosyndesis—Pairing between chromosomes of maternal and paternal origin in a polyploid.

Amitosis—Direct division of the nucleus which does not involve the formation of chromosomes.

Amphidiploid—A hybrid with the diploid set of chromosomes of both the parental species. Generally the species hybrid proves sterile : but by doubling of chromosomes and formation of amphidiploid fertility is restored, *e.g.*, AA $\times$ BB gives AB as hybrid and AA BB is the amphidiploid.

Anaphase—A stage in cell division at which the daughter chromosomes move to opposite poles.

Androgenesis—The growth of an individual from a male cell.

Aneuploid—An unbalanced polyploid with one or more chromosomes in excess or deficiency over the diploid complement, *e.g.*, trisomic (2n+1), monosomic (2n—1).

Anthesis—The opening of a flower bud and the time of fertilisation.

Apogamy—The development of a sporophyte from a gametophyte without fertilisation. This is a vegetative process.

Apomixis—Vegetative reproduction in the reproductive organs without sexual intervention. Without fertilisation seed-like organs are formed. It is equivalent in effect to clonal propagation.

Apospory—The development of a gametophyte without the formation of spores.

Asexual—Referring to reproduction which does not involve formation of gametes and fertilisation.

Asynapsis—Non-pairing of chromosomes at meiosis.

Autopolyploid—A polyploid derived by doubling of chromosomes in a homozygous diploid.

Autosomes—Those chromosomes which do not normally affect the determination of sex (cf. sex chromosomes).

Autosyndesis—Pairing between chromosomes derived from the same parent.

Back-cross—Crossing the F_1 hybrid with one of the parents. This may be done to test the gametic ratio of F_1 or to transfer specific gene-complex from one species to another.

Basic number—Generally represented by x, it denotes the haploid number of chromosomes of a diploid ancestor of a polyploid.

Bimodal curve—A frequency curve with two distinct modes or peaks.

Biometry—Measurement of quantitative characters and statistical interpretation in biological problems.

Biotype—An elementary stable form.

Bivalent—Association of two homologous chromosomes held together by chiasmata at the first meiotic division.

Blending inheritance—Due to lack of dominance or control by a large number of genes, F_1 appears intermediate in type between the two crossing parents and there is no clearly defined F_2 segregation. Such characters were once mistaken as non-mendelian or blended.

Bud-mutation—A mutation in the bud. Such a mutated bud may grow into a branch or flower differing in one or more characters from the parent plant.

Cell—It is " the building blocks of living organism ". It is the unit of structure and functions. In plants the cytoplasm encloses cell contents and nucleus and the whole cell is surrounded by cell-wall.

Centromere—A particle in the chromosome thread which determines the repulsion and movement of chromosomes at cell division.

Certation—Competition in rate of growth of pollen tubes of different genetic types.

Character—A term to designate form, function or feature of an organism Genes have predominant effect in the development of a character. Genes do not change except by mutation ; but the character is somewhat variable due to environment. The character is the resultant of interaction between the genotype and environment in the course of development.

Chiasma—The point of exchange of partners in paired chromatids.

Chiasmatype theory—The theory of Jannsens relating to chiasma formation in meiosis.

Chimera—A plant whose tissues may be of two genetically distinct types.

Chromatid—A half chromosome of a longitudinally split chromosome. The two halves separate from each other at anaphase in mitosis and at anaphase II in meiosis. After separation the chromatid is termed a daughter chromosome.

Chromatin—The substance of a chromosome that deeply stains during cell division.

Chromomere—The smallest particle of characteristic size and position on a chromosome. This is especially identifiable on salivary gland chromosomes.

Chromonema—The thin threads of chromosomes to which the chromomeres are attached.

Chromosome map—A diagram to bring out the relative position of genes on a chromosome.

Chromosomes—Thread-like bodies which are distinct in their structure and which make their appearance in the nucleus during cell division. They carry the genes in a linear constant order in a species. Their number is generally constant for a species.

Chromosome theory—The theory according to which the Mendelian factors or genes are located on chromosomes. The chromosomes are the physical bases for heredity.

Clone—A group of organisms descended by vegetative propagation of a common ancestor.

Colchicine—An alkaloid from *Colchicum autumnale* (Liliaceae).

Compatible—Capable of fertilisation.

Complementary factors—Factors, which individually have similar effect but when together cause a different effect. The F_2 segregation shows 9 : 7 ratio.

Congenital—Present at birth.

Constriction—An unspiralised segment of fixed position in a chromosome.

Crossing-over—Exchange of segments between pairing chromosomes by breakage and reunion of corresponding chromatids. This results in the recombination of factors linked in the parents.

Crossing-over—illegitimate :—Crossing-over between homologous segments of two chromosomes which due to non-homology of the rest of the segments do not normally pair.

Cross-pollination—The deposition of pollen from the anther of one flower to the stigma of another.

Couplings—In linkage, the association of characters in inheritance (cf. repulsion).

Cytoplasm—The protoplasm between the cell wall and the nucleus in which the cell contents including nucleus are imbedded.

Darwinism—The hypothesis of Darwin according to which evolution of new species is by the accumulation of small changes. "Natural selection" and "survival of the fittest" play an important role in this.

Daughter cells—Young cells derived by the division of older cell (mother cell).

Daughter chromosome—*See* chromatid.

Deficiency—Loss of an acentric segment from the end of chromosome of a diploid set.

Deletion—Loss of a segment from the intercalary portions of a chromosome.

Determinant—The hypothetic element which according to Weismann is situated on the chromosome and controls development. It is now termed 'gene or factor'.

Diakinesis—The stage in meiosis following diplotene.

Dicentric : A chromosome or chromatid with two centromeres.

Dichogamy—The maturation of the two sexes at different periods to ensure cross-pollination.

Dihybrid—A hybrid in respect of two pairs of allelomorphs.

Dioecious—Unisexual male and female elements in different plants.

Diploid—**2n** or somatic number of chromosomes. An organism with **2n** chromosomes.

Diplotene—The stage in meiosis following pachytene.

Disjunction—The separation of paired chromosomes at anaphase I of meiosis.

Disomic—Two homologous chromosomes or genes.

Dispermic—Fertilised by two sperms.

Distal—The part of chromosome farther from centromere.

Dominant—When two parents with contrasting characters are crossed, the character of one parent appears in F_1 to the exclusion of the character of the other parent even though both the factors are present in the hybrid. The factor which expresses itself is said to be "dominant" over the other "recessive".

Duplex—Having two dominant genes—used in polyploids (*e.g.* AAaa of an autotetraploid).

Duplicate factors—Two factors which individually or in combination produce the same phenotypic effect. In F_2, 15 : 1 ratio is obtained.

Duplicate genes—Two pairs of genes having the same effect. One dominant gene shows the same effect as when both the dominant genes are present and the double recessive alone brings out the recessive character. F_2 ratio 15 : 1.

Duplication—The condition in which a segment occurs twice in the same chromosome or complement.

Dyad—Two cells which result from the first division of meiosis (cf. tetrad).

Ecotype—A stable form of a particular region.

Egg—The female germ cell. In higher plants it is enclosed in the embryo sac of the ovule.

Emasculation—Removal of stamens before they burst and shed their pollen.

Embryosac—One of the tetrads from F. M. C. representing female gametophyte of angiosperm.

Endosperm—Nutritive tissue in the embryosac. It is constituted by triploid tissue arising out of "double fertilisation".

Environment—Attendant or surrounding factors which affect development of an organism.

Epigenesis—The concept now accepted according to which the embryo is developed fresh in each generation. This is in contrast to the hypothesis of preformationists according to which the egg merely unfolds the character already present in it in a microscopic form.

Epistasis—The suppression of the effect of one gene by another which is not allelomorphic to it. Thus 'pearly' appearance in cholam is suppressed by 'red' colour. The consequent F_2 ratio is 12 : 3 : 1.

Equational division—The second division of meiosis where the sister chromatids are separated.

Equatorial plates—During metaphase of cell division, chromosomes lie at the equator of the spindle. This appearance is termed equatorial plate.

Eugenics—The application of the principles of heredity to human race.

Euploid—An organism with chromosome number in exact multiple of the haploid number. It may be diploid, triploid, tetraploid, etc.

F_1—First filial generation. The first generation off-spring or hybrid of a cross.

F_2—The second filial generation. The inbred grand-progeny of a cross produced by selfing or inter-se crossing of F_1.

Factor—The "something" which Mendel hypothesised as present in cells and which determines the development of character. It is the unit of Mendelian inheritance and is the abstract form of 'gene' or 'chromomere'.

Fertile—Capable of producing fruit.

Fertilisation—The fusion of the nuclei from male and female gametes.

First Division—First division of meiosis. It is also termed reduction division or heterotypic division.

Fluctuating variation—Variation in an individual due to environment.

Gametes—Germ cells.

Gametophyte—The plant which represents the haploid generation in the alternation of generation and which gives rise to gametes.

Gene—Same as factor. It is the unit of crossing-over. By interaction of gene complex with cytoplasm and environment, character is developed. Allelomorphs are located in corresponding loci of homologous chromosomes. The genes are arranged in a constant linear order on chromosomes. They constitute "the physical basis of heredity".

Genetics—"Genetics is the science which seeks to account for the resemblances and differences which are exhibited by organisms related by descent" (By Babcock and Clausen). It is a science dealing with physiology of heredity and variation.

Genome A chromosome set.

Genotype The hereditary properties of an organism as represented by the gene constituents. They may be expressed or latent (cf. phenotype).

Gigas form—Giant form.

Graft hybrid—Strictly, graft chimera : a plant arising from graft union and comprising distinct types of tissues from the stock or scion.

Haploid—A true haploid is an organism with one set of chromosomes.

Heredity—"Heredity is genetic continuity of germinal material between parents and offspring" (Babcock and Clausen).

Heterochromatin—Parts of chromosomes which stain to different degrees from the rest.

Heterogamy—Differentiation of male and female gametes.

Heteroploid--An organism with chromosome number which is not an exact multiple of the haploid number (cf. Euploid).

Heterosis--Same as hybrid vigour.

Heterotypic division—The first division of meiosis in which the homologous chromosomes are separated to opposite poles causing the reduction in chromosome number.

Heterozygote—A zygote formed from the union of two gametes which differ in their chromosome constitution.

Hexaploid—An organism with chromosomes six times the haploid number.

Homology—Similarity in the structure of plant organs or chromosomes which is due to their descent from a common ancestor.

Homotypic division--The second division of meiosis.

Homozygote.—A zygote from the gametes where the chromosomes are of identical constitution.

Hybrid—An organism developed by the fusion of dissimilar gametes, *i.e.*, a heterozygote.

Hybrid sterility--Sterility of the hybrid (F_1).

Hybrid-structural--A hybrid formed by the fusion of gametes whose chromosomes showed structural differences.

Hybrid vigour—Vigour exhibited by a hybrid.

Hybridisation--Crossing plants or animals of unlike hereditary constitution.

Hyperplasia—Abnormal growth due to undue cell division.

Hypostasis- The condition in which a gene is suppressed by another one not allelomorphic to it. In a case of epistasis, the suppressed gene is said to be hypostatic to one that suppresses (epistatic).

Illegitimate crossing over--*See* Crossing-over.

Inbreeding--Mating of related plants. This is done by 'selfing' hermaphrodite flowers. Inbreeding increases homozygosity in further generations of inbred-line.

Incompatible—Incapable of fertilisation.

Independent assortment--The second law of Mendel according to which the segregation of one pair of factors is independent of segregation of any other pair.

Inhibiting factor—A factor which inhibits the phenotypic expression of another factor. In F_2, 13 : 3 ratio is observed.

Interchange--Exchange of segments between non-homologous chromosomes by illegitimate crossing over.

Interference—The phenomenon by which crossing-over at one point minimises the occurrence of another crossing-over in its immediate neighbourhood.

Interkinesis—*Interphase or resting stage between two divisions of a cell, but not applied to resting stage in general.*

Interphase—The short resting phase between the first and second division of meiosis.

Inversion—Inversion or reversal of the linear order of genes in a segment of a chromosome. ABFEDCGH shows inversion of CDEF segment of ABCDEFGH.

Isogamy—Morphological similarity between the male and female gametes.

Isolation—Prevention of inter-crossing between a separated section of a species or kind and the rest of that species or kind.

Karyokinesis—Mitosis.

Karyology—The study of the nucleus.

Lamarckism—The hypothesis of Lamarck on evolution which is based on inheritance of acquired characters ; 'use' and 'disuse' of organs play an important role in this. Now, this concept is not accepted (cf. Darwinism).

Law of homologous series in variation—The principle enunciated by Vavilov. In general, closely allied Linnean species are characterised by similar and parallel series of variations ; and as a rule, the nearer these Linneons are genetically, the more precise is the similarity of morphological and physiological variability ; generally nearly related Linneons have consequently similar series of hereditary variation.

Leptotene—The first stage in the prophase of meiosis in which the chromosomes appear as single threads.

Lethal factor—The factor which proves fatal to the normal development of an organism.

Line breeding—A form of breeding technique.

Linkage—The phenomenon by which the parental types appear in greater frequency than expected in F_2. This is due to the location of linked factors on the same chromosome.

Locus (plural : loci).—The position occupied by a gene on a chromosome.

Maternal inheritance—Inheritance where the offspring is after the mother.

Matroclinal—A case where the offspring resembles the mother more than the father.

Maturation—Formation of gametes.

Megaspore—The large spore ; applied to female spores of vascular cryptogams and other higher plants. In Angiosperms applied to embryo sac.

Meiosis—Modified mitosis in which the chromosomes divide once while the nucleus divides twice.

Mendel's Law—The basic principles of heredity enunciated by Mendel (i) that characters form contrasting pairs or allelomorphs—the principle of dominance, (ii) by segregation of genes, the gametes are always pure in respect of an allelomorphic pair—law of segregation, and (iii) the segregation in one pair of allelomorphic genes is independent of the segregation in any other pair, i.e. law of independent assortment.

Mericlinal chimera—An incomplete periclinal chimera.

Metaphase—The stage following prophase in cell division (meiosis or mitosis) in which the chromosomes lie in equatorial plane.

Metaxenia—The influence of male gamete on the developing egg immediately after fertilisation.

Microspore—The male gamete carried in the pollen grain.

Mitosis—The process by which the cell divides into two identical halves by the separation of daughter chromosomes to constitute two identical nuclei.

Modifier—A gene which modifies the expression of another gene.

Monoecious—Unisexual, male and female elements in the same plant.

Monohybrid—The hybrid obtained by crossing two parents differing in respect of a pair of characters.

Monosomic—A diploid lacking one chromosome (2n—1).

Mosaic—An organism in which parts of tissues are genetically different due to mutations occurring during development.

Mother cell—The cell which by meiosis gives rise to tetrad spores (pollen mother cell—P.M.C.—and Embryosac mother cell—E.M.C.—of angiosperms).

Multiple alleles or Multiple allelomorphs—A series of genes any two of which constitute an allelomorphic pair. This arises by repeated mutation of a gene to give different effects. In a diploid organism only a pair of the gene series can exist being located in corresponding loci of the two homologous chromosomes.

Multiple factor—The control of a character by a large number of factors, which may be located at different loci on different chromosomes. In F_2 segregation clear cut classification of phenotypes is not possible.

Multivalent—Association of more than two chromosomes at meiosis.

Mutation—A sudden variation in the gene structure. A mutated gene reproduces itself. The term is widely used to cover gene mutations and other changes due to chromosomal variations such as deletions, duplications, inversions, interchanges, ploidy, etc.

Non-disjunction—The failure of separation of paired chromosomes at meiosis which results in their passing to the same pole.

Normal curve—A graph representing variations which are equally distributed in both the directions. There is a single peak with equal slopes on either side (cf. bimodal curve).

Nucleolar organiser—The part of chromosome that is responsible for the development of nucleolus.

Nucleolus—A body in the nucleus.

Nucleus—A vital constituent of a living cell. It multiplies by mitosis or meiosis. It is highly refractive and deeply staining. It is of specialised protoplasm. It contains chromosomes, karyolymph and nucleolus.

Nulliplex—Having no dominant gene—used in polyploids (*e.g.*, aaaa of an autotetraploid).

Ontogeny—The developmental history of an individual.

Orthogenesis—The doctrine that evolution is by a purposive variation which has a definite course and is determined by the developing organism.

Out-cross—A cross between individuals not related.

Pachytene—A sub-stage in prophase of meiosis at which the chromosomes pair and cross-over takes place at four-strand stage.

Pairing of chromosomes—In meiosis chromosomes come together and lie side by side in zygotene and exchange segments. This association continues to the metaphase stage.

Pangene—The particle hypothesised by Darwin in his Pangenesis Hypothesis to explain variation and evolution.

Parasynapsis—The association of chromosomes by their lying side by side along their length at zygotene of meiosis (cf. Telosynapsis).

Parthenocarpy—The production of fruit without fertilisation and formation of normal seeds, *e.g.*, bananas.

Parthenogenesis—Development of an individual without fertilisation of egg.

Partial dominance.—A case where dominance is not complete and the hybrid is intermediate in type between the two parents. In F_2 1 : 2 : 1 ratio is expected in a monohybrid.

Patroclinal—A case where the off-spring is more after the father than the mother.

Pentaploid—An organism with chromosome number five times the haploid number.

Periclinal chimera—A chimera in which the outer ring of tissues is genetically different from the inner ring.

Phylogeny—The developmental and evolutionary history of a species or genus.

Phenocopy—The resemblance of one species to that of another due to the effect of environment during development, studied by Goldschmidt in insects.

Phenotype—The external appearance produced by the interaction of genotype with environment.

Plastid—One of the living inclusions of a plant cell. It is a bit of specialised protoplasm and is a centre of chemical activity.

Plastid inheritance—Inheritance of characters transmitted by plastids in the ovum. The inheritance is extra nuclear and non-mendelian. Many variations belong to this type.

Pleiotropism—Multiple effect of a gene.

Pollination—The act of transferring pollen grain to the stigma.

Polyhaploid—An organism whose haploid number truly consists of more than one set of chromosomes.

Polyploid—An organism with more than two sets of homologous chromosomes. They may be triploid (3n), tetraploid (4n), etc.

Polysomic—Addition of some chromosomes of a set to the diploid complement.

Polyspermy—The entrance of more than one sperm into the ovum.

Position effect—Phenotypic effect arising from the change of position of genes.

Precocity theory—The theory of Darlington which characterises meiosis as due to precocious onset of prophase before the longitudinal division of chromosomes during the resting stage.

Pre-formation—The hypothesis of some old biologists who believed that the egg unfolds the characters already present in it in a microscopic form (cf. epigenesis).

Prophase—The first stage of mitosis or meiosis from the appearance of chromosomes to metaphase.

Protandry—The ripening of the androecium before the gynaecium.

Protogyny—The ripening of gynaecium before the androecium.

Protoplasm—" Physical basis of life." A complex chemical compound defying structural analysis.

Proximal—The part of the chromosome nearer to centromere.

Pseudogamy—Parthenogenetic development of the egg which requires stimulation from the male gamete, but there is no true fertilisation.

Pure-lines—A strain of plants which are rendered comparatively homozygous by continued selfing.

Quadriplex—Having four dominant genes—used in polyploids (*e.g.*, AAAA).

Quadrivalent—The association of four chromosomes in meiosis.

Recessive—*Vide* dominant.

Reciprocal cross—Refers to two crosses in which the male parent of one is the female parent of another and *vice versa e.g.*, A × B and B × A.

Recombination—The phenomenon by which the characters found distributed in the parents are combined into an offspring by hybridisation.

Reduction division—Meiosis.

Replication—Repetition of treatments in an experiment to eliminate errors due to soil, etc.

Repulsion—In linkage the appearance of the two dominant characters distributed in the two parents.

Restitution nucleus—The nucleus which is formed by the failure of separation of chromosomes in the first division of meiosis.

Ring chromosome—Association of chromosomes end to end to form a ring in meiosis.

Rogue—A variation from the type.
v. To remove rogues.

Satellite—A chromosome segment separated by a long constriction.

Secondary association—Lying together of bivalents in meiosis. An indication to the polyploid nature of the organism.

Secondary sexual character—A character associated with the sexual chromosomes of male and female but has nothing to do directly with reproduction.

Sectorial chimera—A chimera in which the tissues of different genotype appear in distinct sectors (cf. periclinal chimera).

Selection—The choice of certain individuals for purposes of propagation, from a mixed population where the individuals vary in characters.

Selection-artificial—Man selects certain variants consciously for his economic advantage though such selected individuals may not survive natural selection.

Selection-natural—Under natural conditions, certain individuals survive the severity of adverse conditions while others are extinguished. The surviving ones are the ' fittest ' while the extinct ones are unfit.

Selfing—The act of artificially self-pollinating the flowers.

Sex chromosomes—Chromosomes with particularly determine sex (cf. autosomes).

Sex limited—The expression of a character limited to one sex.

Shift—The phenomenon by which the extracted types from F_2 are not exactly the same as parents in respect of any quantitative character. They are slightly different from the parents.

Sib or Sibling—Progenies of the same parents but of different birth.

Simplex—Having one dominant gene—used in polyploids. (*e.g.* Aaaa of an autotetraploid).

Somatic—Referring to body tissues as distinct from gametic cells.

Somatic mutation—Mutation in the somatic cells.

Somatoplastic sterility—Sterility caused by hyperplasia of nucellus or inner integument of ovules after fertilisation.

Spermatogenesis—The formation of male germ cells.

Spindle—In stained cytological preparations of dividing cells the appearance of thread like structures in the form of spindle running from pole to pole. The chromosomes are attached to the threads at the region of spindle attachment or centromere. The spindle appears at metaphase stage and is responsible for the later movements of chromosomes to the poles.

Spore mother cell—The first cell which by division gives rise to spores.

Sporophyte—The diploid spore-forming generation of plants in which various degrees of alternation of generation is noticed.

Sport—A mutant type especially from plant buds.

Standard deviation—A statistical constant to measure dispersion round the mean.

Synapsis—The pairing of homologues to form bivalents.

Syngamy—Fertilisation ; *e.g.* union of the male and female gametes to form the zygote.

Telosynapsis—The association of chromosomes end to end. (The pairing is now taken to be parasynaptic).

Tetrad—The formation of 4 daughter cells by meiosis. The four strand stage of chromosomes in diplotene.

Tetrasomic—An organism in which one chromosome is repeated four times while the rest are in twos. The somatic chromosome number then is $2n+2$.

Trait—A loose synonym of "character."

Transgressive variation—The variation appearing in F_2 segregation of a cross where the progenies show more extremes of variation than is present in the parents. This is due to cumulative effect of favourable genes originally distributed between the parents.

Translocation—The attachment of a segment of a chromosome to another place in the same chromosome or different chromosome.

Trihybrid—A hybrid in respect of three pairs of genes.

Triplex—Having three dominate genes—used in polyploids (*e.g.* AAAa of an autotetraploid).

Triploid—A polyploid with three haploid set ($3n$) of chromosomes.

Trisomic—A polysomic in which one chromosome of the haploid set is repeated thrice.

Trivalent—Association of three chromosomes in meiosis.

Unit character—A character which behaves as a unit in inheritance and is governed by a single pair of allelomorphs.

Univalent—The unpaired single chromosome of meiosis.

Variation—"Variation is difference whether in the expression of somatic characters or in the elements of the germinal substance exhibited among groups of organisms related by descent" (Babcock and Clausen).

Vegetative reproduction—Asexual reproduction by buds, layering, cutting, etc., without the intervention of formation of gametes and fertilisation.

V'-chromosome—Where the female is heterozygous sex, the sex chromosomes are designated *wz* (cf. *xy* chromosomes).

X-chromosome—The sex chromosome of the *xy* type where the male is heterozygous for sex (cf. *wz* chromosomes).

Xenia—The immediate effect of pollen on the endosperm characters of the crossed seed.

Y-chromosome—The sex chromosome of the *xy* type where male is heterozygous, *xx* being female *xy* being male.

Zygote—The cell that results from the fusion of the gametes.

Zygotene—The second sub-stage in the prophase of meiosis. At this stage the chromosomes in single thread come to lie side by side.

APPENDIX VII

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